



Do Chimpanzees Predict Others' Behavior by Simulating Their Beliefs?

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Abstract – Recent studies have shown that great apes predict that other agents will search for objects of interest where the agents believe the objects are hidden. Little is understood about the cognitive process that apes undergo to make such predictions. According to prevailing models, great apes make such predictions by metarepresenting others' beliefs or perceptual states. We investigated the simpler simulation model. In this model, apes predict where other agents will search for objects of interest by simulating believing what another agent believes about the location of the object. The simulation model predicts that simulating what another believes should manifest in altercentric biasing effects, such as behaving as if one shares another's belief in cases where the other's belief is false. We tested this by giving chimpanzees a novel search paradigm embedded in a change-of-location false-belief test and measured where they searched for a grape that they witnessed moved from its original location to a new location. In true-belief trials, chimpanzees were presented with an agent who knew (as they did) that the grape was hidden in the new location; in false-belief trials, the agent falsely believed the grape was still hidden in the original location while the chimpanzee knew it was hidden in the new location. As predicted by the simulation model, chimpanzees searched for the grape closer to its original location than to its new location in significantly more false-belief trials than true-belief trials. Results suggest that chimpanzees show a signature altercentric biasing effect of simulating believing what others believe and may use simulation, rather than metarepresentation, to predict where others will search for objects of interest.

Keywords – Simulation, Metarepresentation, Altercentric biasing effect, False-belief task, Theory-of-mind, Empathy, Chimpanzees

Several recent theory-of-mind (ToM) studies have shown that great apes predict that other agents will search for objects of interest where the agents have evidence to believe the objects are hidden (Buttelmann et al., 2017; Kano et al., 2019; Krupenye et al., 2016; Schmelz et al., 2011; Schmelz et al., 2012). In each of these studies, apes observed another agent being presented with contextual evidence that an object of interest was hidden in a particular location. The evidence in some of these studies was perceptual (e.g., the agent was shown the object hidden in the location) and in others, it was inferential (e.g., the agent is shown something, such as a slanted board, that indicates that the object is hidden in that location). Various behavioral measures (e.g., anticipatory looking, helping behavior, and competitive choice selection) indicated that the apes predicted the agents would search for the objects where the agents had evidence to believe the objects were hidden. These ToM studies, however, leave unanswered what

cognitive process and representational format apes employ to make such predictions. A prevalent explanation of the data is the metarepresentation model in which apes are taken to represent other agents as having beliefs (a type of reality-incongruent mental state) about the location of objects and predicting that agents will search for objects where the agents are thought to believe the objects are hidden (Horschler et al., 2020). In this model, apes that represent that an agent has the belief that an object is in location *x* will predict that the agent will search in location *x*.

One model that has not been considered is the simulation model in which apes predict where other agents will search for objects of interest by simulating (imagining) believing what another agent believes about the location of the object and predicting that the agent will search where the ape imagines searching while simulating the belief (Goldman & Jordan, 2013; Gordon, 1986). In the simulation model, apes that imagine searching in location *x* while simulating believing the object is in location *x* will predict that the agent will search in location *x*.

A critical difference between the metarepresentation and simulation models is the representational formats used in these models and the different effects these representational formats have on a subject's own behavior toward the environment. In the metarepresentation model, subjects represent another agent's belief that, for example, food is behind the tree, not by adopting or simulating the first-order belief that food is behind the tree, but by having a second-order belief (a representation) that the other agent believes (represents) the food is behind the tree – that is, by having a representation about a representation or metarepresentation (Perner, 1991; Pylyshyn, 1978). A distinguishing feature of metarepresentation is that it provides a detached method of representing others' mental states that does not involve sharing or imaginatively believing what others believe about the environment (Gallese & Goldman, 1998). Metarepresentations are representations about the unobservable mental states (e.g., beliefs, perceptions, feelings) inside other agents; they are not first-order representations about the physical, observable environment. As a result, metarepresentations by themselves, independent of one's first-order representations about the physical, observable environment, are not expected to affect how one interacts with this environment. This is not to say, of course, that one cannot have both first-order representations about the physical, observable environment and metarepresentations about the unobservable mental states in others. However, in such cases, it is one's first-order representations about the environment that guide one's behavior through this environment, not one's metarepresentations about others' mental states. It is your first-order knowledge that the food is behind the tree, for example, that guides you to search for the food behind the tree, not your metarepresentational knowledge that another agent also believes that food is behind the tree. The function of first-order representations about the physical, observable environment is to guide one's behavior through that environment, whereas the function of metarepresentations is to provide a way to predict other agents' behavior (e.g., predicting that the agent will search behind the tree). It is this detached feature of metarepresentations that allows for representing others' beliefs and mental states and predicting others' behaviors without the process affecting one's own behavior toward the environment.

In the simulation model, by contrast, simulating believing information that another agent believes about the environment is a decidedly engaged cognitive process. It necessarily involves the use of first-order representations of the environment that are similar to ('mimic') the content of first-order representations that encode other agents' actual beliefs about the environment (Goldman & Jordan, 2013). While the process of simulating believing what another agent believes about the environment may be done deliberately, consciously, and with accompanying metarepresentational states (what Goldman [2006] calls 'high-level simulation'), it often occurs automatically, implicitly, and without the use of metarepresentational states ('low-level simulation' [Goldman, 2006]), similar to what occurs in cases of automatic affective empathy. Neurological studies on automatic affective empathy show that merely observing evidence that another agent is receiving a pain-inducing stimulus (e.g., observing a needle pricking another person's finger) automatically causes subjects to enter pain-related brain states that are similar to (i.e., simulate) the pain-related brain states of the observed agent (Morrison et al., 2004; Singer et al., 2004). Subjects in these studies do not consciously intend to empathize with the other agent; rather, the empathic responses occur automatically and without conscious intention. In addition, the pain-related brain states that occur in subjects are not metarepresentational states – they do not represent that another

agent is experiencing the mental state of pain. Although the process of automatic affective empathy may subsequently cause subjects (such as adult human beings) with metarepresentational capacities to attribute the mental state of pain to others, the process itself does not necessarily involve metarepresentational states, as is evidenced by the fact that automatic affective empathy occurs in rodent species that are not known to have metarepresentational capacities (Carrillo et al., 2019).

According to the simulation model, a similar low-level simulation process occurs when subjects simulate believing something that others believe. That is to say, the mere observation of another agent in a belief-inducing situation automatically causes (without any intervening metarepresentational states) a subject to enter a first-order representational state (a state of simulated believing) that is similar in content to the first-order representational state that encodes the other agent's actual belief. For example, on the simulation model, low-level simulation of this kind putatively occurs frequently in theatergoers. While observing a character on the stage, we often spontaneously imagine believing things that the character believes. We know that the monster-like figure that slipped into the closet while the main character was not looking is not a real monster, for example, but the moment the character opens the closet door, we feel like screaming (and may do so) and expect a similar reaction from the character on stage. This does not happen because we actually believe there is a monster in the closet, as we know full well that the figure in the closet is not a monster. Rather, according to the simulation model, this happens because we automatically imagine believing what the character believes – that the figure in the closet is a monster. In this example, it is clear that our simulated belief that there is a monster in the closet is not a metarepresentational state as it does not represent anyone having a mental state. Such automatic, implicit, non-metarepresentational simulation also putatively occurs in real-life situations. For example, on the simulation model, you may know that the cookie jar is empty, but the moment you see a child look at the cookie jar you spontaneously imagine believing what the child believes – that there are cookies in the jar. This causes you to imagine reaching in the jar and being surprised that it is empty, which is the same behavior and reaction you expect from the child. Again, this low-level process of simulation occurs quite automatically and implicitly, and it does not involve metarepresentations; your imagined belief that there are cookies in the cookie jar is not a metarepresentational state.

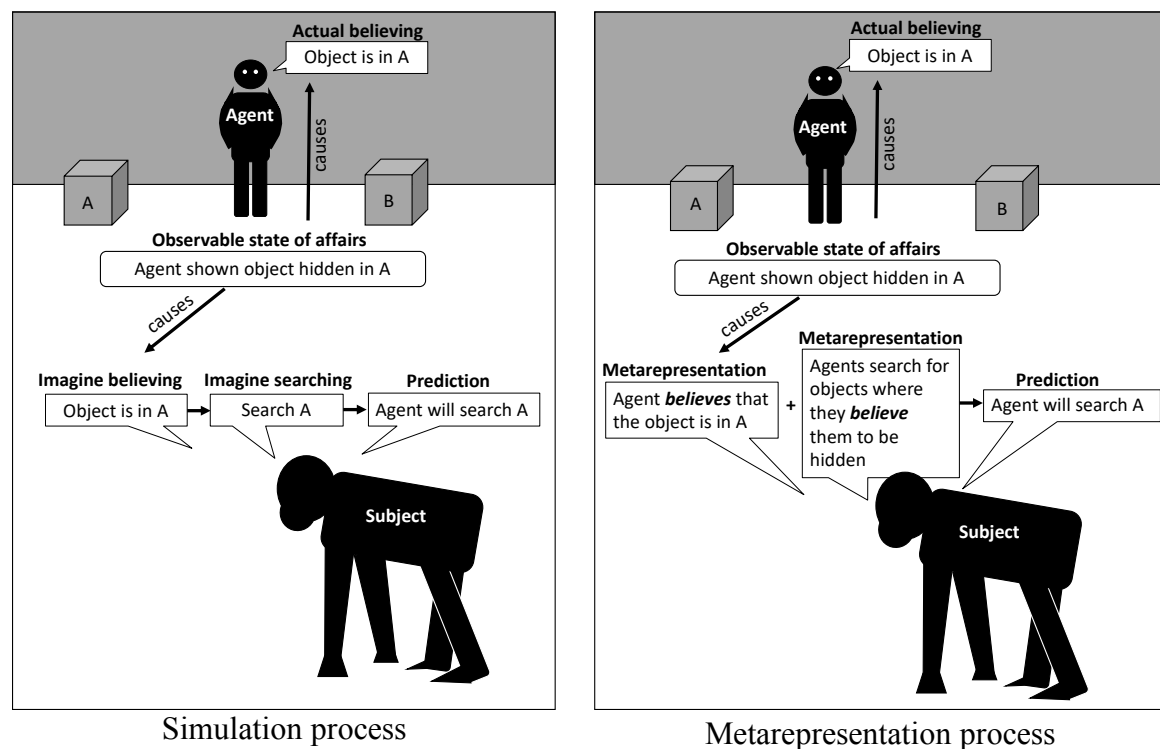
To summarize the simulation model in more formal terms, a subject automatically and implicitly simulates believing information that another agent believes if (i) the subject is in a state of imagining believing some information *p* (e.g., that there are cookies in the cookie jar); (ii) this state of imagining believing *p* is directly caused (without intervening metarepresentations) by observing the agent encountering a stimulus that is evidence for *p* (e.g., the agent looking at a jar that is indicative of cookies inside); and (iii) this state of imagining believing *p* is similar in content to the actual belief the agent has when encountering the stimulus that is evidence for *p*. The examples given above demonstrate that simulating believing what another agent believes does not require the use of metarepresentational states. Of course, this is not to deny that deliberate, conscious acts of simulation by subjects with metarepresentational capabilities may cause such subjects to attribute mental state to other agents. What the simulation model holds, however, is that automatic, implicit, and non-metarepresentational simulation also occurs in humans, and it is this kind of low-level simulation that occurs in apes.

According to the simulation model, the simulation process in apes is an implicit, non-metarepresentational process that is automatically triggered when observing other agents encountering stimuli that induce beliefs in those agents. In Krupenye et al.'s (2016) change-of-location false belief study, for example, apes observe another agent being shown an object being hidden in container A. This evidence presented to the agent causes the agent to believe the object is in container A. While the agent is absent, the object is removed from container A, placed in container B, and then removed from container B. Removing the object from container A makes the agent's belief that the object is in container A false (reality incongruent). After the object has been removed from container B, the agent returns to the containers but gives no immediate behavioral indication about which container he will search inside for the object. The apes watching this scene, however, show signs of expecting the agent to search in container A by looking first at container A (rather than at container B) when the agent returns. According to the simulation model, apes make this prediction in the following way: Observing the agent being shown the object hidden in

container A directly causes (without intervening metarepresentations) the apes to imagine believing the object is in container A, which causes them to imagine searching in container A, which causes them to expect the same reaction from the agent (see Figure 1, left panel). As noted above, this process is taken to occur implicitly, automatically, and without any metarepresentations. In imagining believing that the object is in container A, the apes are in a first-order representational state that is similar in content to the actual belief the agent is in. In contrast, according to the metarepresentation model, apes employ metarepresentations – they “attribute reality-incongruent mental states” to the agent (Krupenye et al., 2016, p. 113) – to predict the agent’s behavior. According to the metarepresentation model, observing the agent being shown that the object is in container A causes the apes to attribute to the agent the reality-incongruent mental state of believing that the object is in container A. With their metarepresentational knowledge about the agent’s belief, plus their general metarepresentational knowledge that agents search for objects where they believe them to be hidden, the apes predict that the agent will search in container A (see Figure 1, right panel). It should be noted that the metarepresentation process in apes is also taken to occur implicitly and automatically (Krupenye et al., 2016).

Figure 1

Simulation and Metarepresentation Explanations of the Krupenye et al. (2016) Study



Note. In the left panel, the subject predicts that the agent will search in container A by a simulation process. In the right panel, the subject predicts that agent will search in container A by a metarepresentation process.

Simulated beliefs, according to simulation theorists (Gallese & Goldman, 1998), are never entirely ‘off-line’ (inhibited) and often affect a subject’s behavior much in the way actual beliefs do (e.g., simulating believing there is a monster in the closet may actually cause you to scream just like actually believing there is a monster in the closet would). Thus, a signature side effect of predicting another agent’s behavior by simulation is that the simulation process has the potential to affect one’s own egocentric behavior toward the environment in situations where one is simulating believing something that conflicts with one’s own true belief about the environment. As an illustration, suppose that another agent falsely believes the food is

in location x , but you correctly believe the food is in location y . Further, suppose you simulate believing what the agent believes in this situation, which means you simulate believing that the food is in location x . In this situation, you are in conflicting first-order representational states about the location of the food. Your simulated belief is a first-order state that represents that the food is in location x , but your true belief is a first-order state that represents that the food is in location y . Since first-order representational states about the environment guide one's search behavior toward the environment, and simulated beliefs are never entirely off-line, this conflict between your simulated belief and your true belief has the potential to bias your own search for the food. Because your simulated belief is a first-order representation that the food is in location x , it has the potential to influence you in your search for the food, potentially biasing you to search away from location y (where your true belief represents the food) and toward location x (where your simulated belief represents the food). In contrast, because of the detached nature of metarepresentations discussed above, the metarepresentation model does not predict a search bias in situations where another agent has a false belief about the location of a hidden object. Thinking that the agent falsely believes the food is in location x is not a first-order representation that the food is in location x – it is a metarepresentation about the mental state of belief in the agent. As a result, it is not expected to influence one's search behavior for the food.

On the simulation model, then, simulating believing what another agent believes when it conflicts with one's own true belief about the environment predicts a signature altercentric biasing effect on one's own behavior toward the environment, causing one to behave toward the environment as if one shared the other agent's false belief. Altercentricism is the biasing effect that another's point of view has on one's own egocentric cognition and behavior (Kampis & Southgate, 2020). A recent series of ToM studies with adults and infants supports this prediction (Bardi et al., 2017; Deschrijver et al., 2016; Kaddouri et al., 2020; Kovács et al., 2010; Kovács et al., 2014; Nijhof et al., 2017). These studies show that while implicitly tracking the beliefs of another agent, subjects behave (in terms of their reaction time) as if they actually shared the belief of the other agent. Specifically, they found that subjects who believed that a particular object was absent were nevertheless surprisingly faster to indicate the object's presence, once it was revealed, if they were paired with an agent who believed the object was present. Thus, subjects behaved as if they shared the other agent's belief that the object was present. This is exactly what would be expected were subjects simulating believing what the other agent believed about the presence of the object. By simulating believing that the object is present, subjects are in a first-order representational state that is identical in content to actually believing that the object is present; as a result, the simulated belief that the object is present is expected to produce behavior in subjects similar to actually believing the object is present (see Goldman & Jordan, 2013). In line with these findings, a recent neurological study (Kampis et al., 2015) indicates that when infants are presented with another agent who falsely believes that an object is present, they undergo neurological processes that are strikingly similar to those they undergo when actually believing that an object is present. Again, this is what one would expect were infants using their own first-order belief system to simulate believing what the other agent believes about the object's presence.

Notwithstanding their differences, both the metarepresentation model and the simulation model are capable of explaining how apes successfully predict where agents with beliefs about the location of an object will search for the object. Nevertheless, there are three points that antecedently favor the simulation model over the metarepresentation model. First, the simulation model offers a simpler explanation of the ape data referenced above, as well as data from similar false-belief studies with infants (Buttelmann et al., 2009; Southgate et al., 2007) and monkeys (Hayashi et al., 2020). This is because the model does not credit subjects with the cognitively sophisticated capacity for metarepresentation or general metarepresentational knowledge about agents, such as that agents will search for objects where they believe them to be located. Second, apes have been shown to possess a related form of mental simulation, emotional empathy (Campbell & de Waal, 2011; Hirata et al., 2013; Madsen et al., 2013; Parr, 2001; Parr & Hopkins, 2000; Romero & de Waal, 2010), but have not been shown to possess any capacity to metarepresent other types of reality-incongruent mental states besides belief (Tomasello & Moll, 2013). Third, a number of studies suggest that chimpanzees are capable of imitation and imitation recognition (Bard, 2007; Fuhrmann et al.,

2014; Haun & Call, 2008; Nielsen et al., 2005; Persson et al., 2018; Whiten, 2013), which are socio-cognitive abilities hypothesized to be supported by a neurologically embodied form of simulation, mirror neurons (Iacoboni, 2009). Thus, there is some evidence that suggests a general form of simulation processing, neurologically based in mirror-neuronal systems, that underlies a variety of social-cognitive abilities in chimpanzees (Gallese, 2013; Gallese et al., 2004; Gallese & Sinigaglia, 2011; Pope et al., 2015) but no comparable evidence suggesting a general form of metarepresentation underlying these social-cognitive abilities.

To date, there have been no direct comparative tests of these two models with great apes. The simulation model predicts that apes will show a signature altercentric bias in their own search behavior for an object of interest as a side effect of their predicting where another agent will search for the object of interest in a change-of-location false-belief test. Results from Krupenye et al. (2016), Kano et al. (2019), and Buttelmann et al. (2017) show that just by watching another agent in a change-of-location false-belief scenario, apes spontaneously predict (as evidenced by their anticipatory-looking and deliberate manual behaviors) where the agent will search for an object of interest. The belief-simulation model, therefore, predicts that by watching another agent in a change-of-location false-belief scenario, chimpanzees will use simulation to predict where the agent will search and, as a side effect of this process, will show a signature altercentric bias in their own search behavior for the object. To test for this search bias, we presented chimpanzees with a novel search paradigm embedded in a change-of-location false-belief test. Chimpanzees watched while a grape was first buried in one location ('Original Location') in a trough filled with hay and then dug up and reburied in a new location ('New Location') in the trough. During these trials, an Agent (played by a human experimenter) was present and watching the burying of the grape. In true-belief (TB) trials, the Agent witnessed the burial and reburial of the grape and correctly believed the grape was in the New Location. In false-belief (FB) trials, the Agent only saw the initial burial of the grape and falsely believed the grape was in the Original Location. After seeing the grape reburied in the New Location, the chimpanzees were allowed to search for the grape and eat it. In line with the belief-simulation model, we predicted that chimpanzees would demonstrate a signature altercentric bias in their own search behavior, resulting in more occurrences of searches nearer to the Original Location (where the Agent falsely believed the grape to be) in the FB trials than in the TB trials.

Experiment 1

Method

Ethics Approval

For Experiments 1 and 2, all applicable national, international, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with and approved by the Institutional Animal Care and Use Committee (IACUC) at which institution the studies were conducted (NCCC protocol: 00000894-RN02; YNPRC protocol: YER-2002897-102117GA).

Participants

Forty adult chimpanzees (*Pan troglodytes*), including 20 males and 20 females from the National Center for Chimpanzee Care of The University of Texas MD Anderson Cancer Center (NCCC), participated in the study. Subjects ranged from 21-57 years of age, and the average age was 35.5 years of age. All subjects were socially housed in groups ranging from 2-9 individuals with 24-hour access to indoor/outdoor enclosures (except during cleaning) with bedding, climbing structures, and daily environmental enrichment. Chimpanzees were fed a commercially available primate diet and fresh produce, with daily foraging opportunities and *ad libitum* access to water.

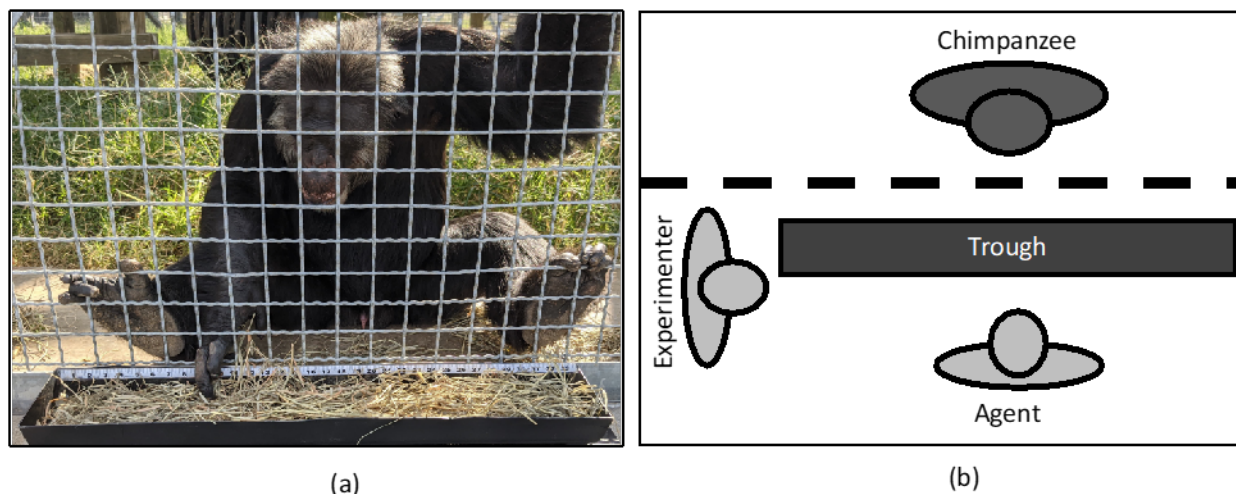
Procedure

Chimpanzees were tested individually in their regular indoor or outdoor enclosure. Chimpanzees were not separated from their social group for procedures; rather, experimenters tested individual chimpanzees who were motivated to participate while groupmates were occupied in another area of the enclosure. A wire mesh separated the chimpanzees and experimenters. Subjects were initially habituated to searching for grapes buried in a plastic flower trough (L: 87.6 cm, W: 15.2 cm; D: 5.7 cm) filled with hay. A tape measure in inches, hidden from the subject's view, was taped to the inside, upper lip of the trough on the side facing the experimenter. This tape measure was used in experimental conditions to record the location where a subject's fingers crossed the lip of the trough as they began to search for the food (see Figure 2a).

Habituation Phase. Before testing, each chimpanzee was given the opportunity to habituate to the trough, which was new to them, and to search for grapes in the hay. In each trial, while the chimpanzee watched, the experimenter buried a grape approximately 2 cm deep in the hay so that it could not be seen and then moved the trough toward the mesh where the chimpanzee was seated. The chimpanzee was allowed to stick its fingers through the mesh, dig up the grape, and eat it. If the chimpanzee was having difficulty locating the grape, the experimenter pointed to the location of the hidden grape and (if this proved unhelpful) removed the surrounding hay to reveal the grape beneath. The habituation was over once the chimpanzee successfully dug up and consumed the buried grape without help on 5-6 consecutive trials. All subjects reached criterion in a single session. Habituation sessions and experimental sessions did not occur in a single session and were separated by a minimum of 3 hours.

Figure 2

General Setup for Experiment 1



Note. (a) Plastic trough used in the study, as seen from the experimenter's perspective. The chimpanzees could not see the measuring tape on the inside edge of the trough from their perspective. (b) Set-up for all experimental and control sessions in experiments 1 and 2. Note that in the habituation phase, the set-up was the same except that the Agent was absent and the experimenter sat opposite the chimpanzee, which made the hiding of the grapes and the moving of the trough easier.

Experimental Sessions. After being habituated to finding grapes in the trough, each subject was given one true-belief (TB) session and one false-belief (FB) session. The TB and FB sessions were designed as a back-and-forth, food-sharing game for finding buried grapes between the chimpanzee and a human (the Agent). Each session consisted of six warm-up trials and a seventh experimental TB or FB trial, depending on the session. Thus, each subject had one TB trial and one FB trial, and the order of

experimental sessions was counterbalanced across subjects. Experimental sessions were separated by a minimum of 3 hours.

Warm-up Trials. The six warm-up trials were designed to familiarize the chimpanzee to the structure of the back-and-forth game with the Agent. The Agent was played by a human researcher (RL, CK, or WH) with no prior experience working directly with or feeding these chimpanzees. In particular, the trials provided the chimpanzees the opportunity to learn that they would be able to search for the grape when the trough was moved toward them but that the Agent would search for the grape when the trough was moved toward the Agent. For the warm-up trials (and all subsequent experimental and control trials), the trough with hay was placed approximately 25 cm away from the front of the mesh, equidistant between the chimpanzee and Agent. The Agent kneeled in front of the center of the trough (see Figure 2b). The trial started once the Agent was kneeling and the chimpanzee was seated in front of the trough. While both the chimpanzee and the Agent watched, a second experimenter buried a grape approximately 2 cm deep in the hay so that it could not be seen. The second experimenter was played by a research assistant (MCM) who had prior experience working with and feeding the chimpanzees. The grape was buried in one of two locations (at either the 8-inch mark or the 25-inch mark on the tape measure), depending on the condition. The hiding location of the grape was pseudorandomized across trials with the stipulation that the grape be buried an equal number of times in each location. While the experimenter hid the grape, the Agent directed his/her head and gaze toward the hiding place and made chimp-like food grunts and head bobs. After the experimenter buried the grape, the Agent faced forward toward the chimpanzee but did not look at the trough. The experimenter then moved the trough either toward the mesh, allowing the chimpanzee to find and consume the grape, or toward the Agent, who would find the grape and pretended to eat it. On three warm-up trials, the chimpanzee was allowed to dig up and consume the grape (Chimp First trials); and on three warm-up trials, the Agent was allowed to dig up and consume the grape (Agent First trials). The order of Chimp First and Agent First trials was pseudorandomized within and across sessions with the stipulation that neither type of trial could have more than two consecutive occurrences within a session. The trial ended once the chimpanzee or the Agent dug up the grape.

True-Belief (TB) Trial. The TB trial began exactly like a warm-up trial. While the chimpanzee and the Agent watched, the experimenter buried a grape in one of the two locations, called the Original Location. The experimenter then dug up the grape and reburied it at the New Location. Thus, if the Original Location was at the 8-inch mark, the New Location was at the 25-inch mark, and vice versa. The Original and New Location were counterbalanced across sessions. While the experimenter moved the grape from the Original Location to the New Location, the Agent tracked the movements with his/her eyes and head and made chimp-like food grunts and head bobs. After the experimenter buried the grape in the New Location, the Agent faced forward toward the chimpanzee and continued to make food grunts and head bobs. Throughout the remainder of the trial, the Agent continued to sit directly in front of the center of the trough and look straight ahead in order to prevent any cuing. At this point, and while the chimpanzee was watching, the experimenter then moved the trough toward the Agent as if he/she would be allowed to search for the grape. This was done to elicit a prediction from the chimpanzee that the Agent would be searching for the grape. However, unlike the warm-up trials, the Agent did not search for or dig up the grape when the trough was moved toward him/her. Rather, while continuing to look straight ahead, the Agent audibly tapped the ground located between the Agent and the trough. The visible and audible display of tapping on the ground was done to make clear to the chimpanzee that the Agent did not stick his/her hand into the trough to search for the grape. Immediately after the Agent tapped the ground, the experimenter moved the trough toward the mesh, allowing the chimpanzee to search for, locate, and consume the buried grape. The trial ended when the chimpanzee dug up the grape.

False-Belief (FB) Trial. The FB trial was exactly like the TB trial except that the Agent turned around and faced away from the trough while the experimenter moved the grape from the Original Location to the New Location. Once the experimenter had buried the grape in the New Location, the Agent turned

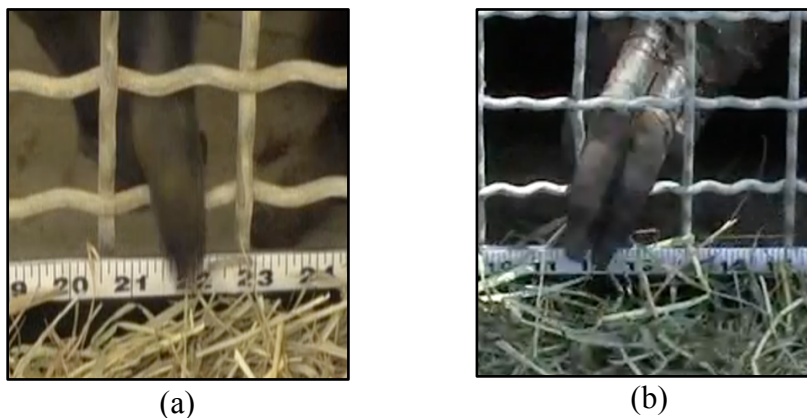
back around and looked straight ahead and continued to make food grunts and head bobs. The trial then proceeded as in the TB trial. The trial ended when the chimpanzee dug up the grape.

Coding

A video camera mounted on a tripod behind the Agent's head recorded the behavior of test subjects in front of the trough in all warm-up and experimental trials. The video recordings of experimental trials were later analyzed by one primary coder (RL) who was aware of subjects and trial type. The aim of the study was to measure the effect that the Agent's belief about the location of the buried grape had on the subject's own search location for the buried grape. In searching for the buried grape, chimpanzees would stick one or two fingers through the mesh and directly rummage through the hay until they located the grape and removed it from the trough using one or two fingers. As a behavioral index of where subjects first searched for the buried grape, we recorded the location to the nearest half inch where the subject's finger(s) first crossed the tape measure lining the inside lip of the trough. Screenshots of the first videoframe showing the subject's finger(s) crossing the tape measure were used to code the location on the tape measure. All finger crossings were also coded live by the experimenter (MCM). The data from the screenshots were used for analysis except in four cases where clear screenshots of finger crossing could not be taken from the video recordings. In those cases, the live coding of the finger crossings was used for analysis. Data from live codings and screenshot codings were highly correlated (TB: $r = .996, p < .001$; FB: $r = .989, p < .001$). In the majority of cases, screenshots showed only one finger crossing the tape measure first (see Figure 3a). In such cases, the location to within a half inch where the finger crossed the tape measure was coded as the location of the finger crossing. In those cases where screenshots showed two fingers crossing the tape measure simultaneously, the midpoint between the two fingers on the tape measure was used to code the location of the finger crossing (see Figure 3b). There were no screenshots showing more than two fingers crossing the tape measure.

Figure 3

Screenshots of Finger Crossings



Note. (a) single-finger crossing (22-inch mark) and (b) two-finger crossing (12-inch mark).

For interrater reliability, 20% of the screenshots of finger crossings were pseudo-randomly selected with the stipulation that half were randomly selected from each type of experimental trial. An independent coder who was naïve to all test conditions was instructed to view the screen shots and determine in ½-inch increments the location of the finger(s) crossing on the tape measure. Interrater reliability was assessed by Spearman's correlation test. Results showed a high interrater reliability ($r = .999, p < .001$). There were only five instances of disagreement, and each involved just a ½-inch difference in judgement. In these five instances of disagreement, the primary coder's data were used for analysis.

Results

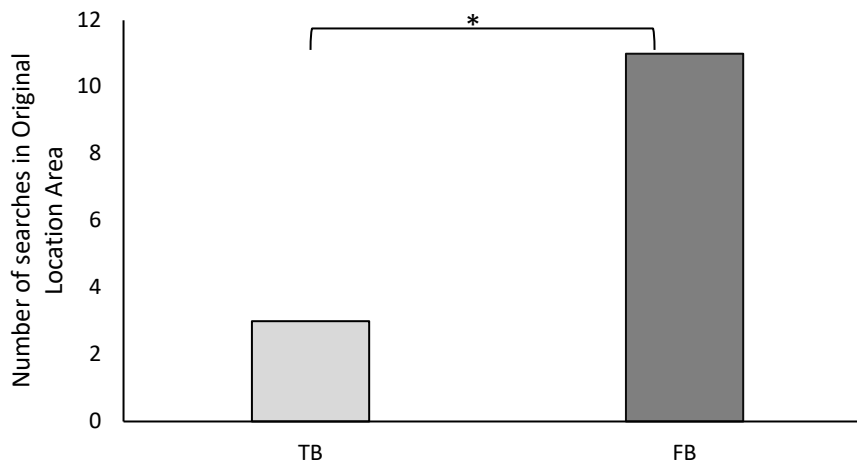
On the simulation model, simulating believing what the Agent's believes about the location of the grape is expected to bias chimpanzees in their own search for the grape, resulting in more searches occurring near the Original Location in the FB trials than in the TB trials. We purposively designed our apparatus to allow for both a dichotomous and a continuous measure of bias, because biases are sometimes detected by using one type of measure but not the other.

On the dichotomous measure of bias, a search was counted as 'near' the Original Location if it occurred on the side of the trough of the Original Location, called the Original Location Area. A bias score was computed relative to the actual New Location of the buried grape, to indicate how far the subject's finger was from the actual New Location of the grape when the finger first crossed the tape measure into the trough. When the actual New Location was the 8-inch mark, a bias score was computed by subtracting 8 from the subject's finger-crossing location (e.g., if finger-crossing was at 10-inch mark, the bias score was +2, and if the finger-crossing was at the 7-inch mark, the bias score was -1). When the actual New Location was the 25-inch mark, a bias score was computed by subtracting the subject's finger-crossing location from 25 (e.g., if the finger crossing was at 20-inch mark, then the bias score was +5, and if the finger-crossing was at the 27-inch mark, then the bias score was -2). Since the midway point between the Original Location and New Location was 8.5 inches, a bias score of ≥ 9 was taken as a search in the Original Location Area, and a bias score of ≤ 8.5 was taken as a search in the New Location Area. Thus, when we refer to the dichotomous bias below, we are referring to any bias score of ≥ 9 , because these scores indicated that the chimpanzee searched in the Original Location Area.

Chimpanzees each received one FB trial and one TB trial. For each condition, we examined how often the apes showed a dichotomous bias (bias score of ≥ 9) by searching in the Original Location Area rather than the New Location Area. There were 11 FB trials in which a dichotomous bias occurred but only 3 TB trials in which a dichotomous bias occurred (Figure 4; see Table 1 in Appendix). As our hypothesis predicted a directional effect in the experiment (more searches in the Original Location Area in FB trials than in TB trials), all p values reported below are one-tailed. Statistical analyses were conducted using SPSS, version 27. An exact McNemar's test showed that the difference in the proportion of FB versus TB trials in which a dichotomous bias occurred was statistically significant ($N = 40$, $p = .011$, one-tailed, effect size = $9/1$ or 9).

Figure 4

Dichotomous Search Bias Results for Experiment 1



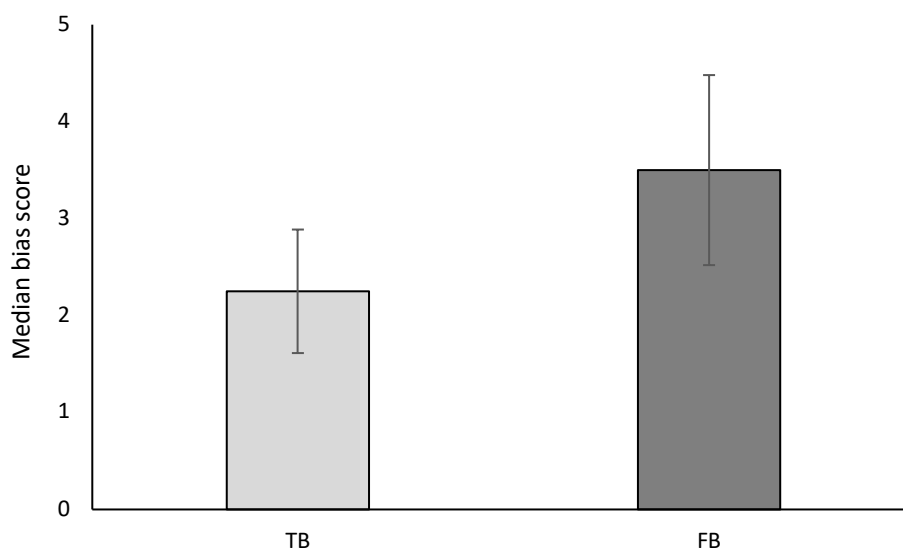
Note. Number of True Belief (TB) and False Belief (FB) trials (out of 40) in which subjects searched in the Original Location Area (bias score of ≥ 9) in Experiment 1. * $p = .011$, one tailed.

It is important to note that while only 28% of subjects (11 out of 40) searched all the way over into the Original Location Area (had bias scores of ≥ 9) in the FB trials, this does not necessarily mean that the majority of subjects were uninfluenced by the Agent's false belief about the location of the grape. It is possible that for many subjects, the influence had a smaller effect on where they searched for the grape, and that a greater proportion of chimpanzees actually searched in a location that was closer to the Original Location in FB trials than in the TB trials.

To assess for this more subtle form of search bias we used the calculated bias scores (described above) to examine a continuous measure of bias. On a continuous measure of bias, subjects showed a search bias if they had a higher bias score in one of the two experimental trials. Of all the subjects, 24 chimpanzees (60%) had higher bias scores in the FB trials than in their TB trials, meaning that they searched closer to the Original Location in the FB trial than in the TB trial. Only 14 chimpanzees (35%) had higher bias scores in the TB trials than in FB trials; and two chimpanzees (5%) had bias scores that were the same in both experimental trials. The median bias score on FB trials was 3.50 inches toward the Original Location, whereas the median bias score on TB trials was 2.25 inches toward the Original Location (Figure 5). This difference across conditions was in the predicted direction and was significant in a Wilcoxon signed-rank test ($Z = -1.641$, $p = .051$, one-tailed, effect size $r = .259$).

Figure 5

Continuous Search Bias Results for Experiment 1



Note. Median bias scores in True Belief (TB) and False Belief (FB) trials, Experiment 1. The bias difference in conditions was significant at $p = .051$, one-tailed. Bars are standard error.

Discussion

The simulation model predicts that chimpanzees should show a biasing effect in their own search behavior in a change-of-location false-belief test. Specifically, the model predicts that chimpanzees should show a greater search bias away from the true location of the food and toward the location where another agent believes the food to be hidden in false-belief trials (in which the agent has a false belief about the location of the food) relative to true-belief trials (in which the agent has a true belief about the location of the food). To test this prediction, 40 chimpanzees were given a change-of-location false-belief test and allowed to search for a grape that they saw moved from the Original Location to a New Location. In TB trials, the Agent correctly believed the grape to be buried in the New Location; in FB trials, the Agent falsely believed the grape to be buried in the Original Location. In line with the simulation model, we

predicted more occurrences of chimpanzees' searching nearer to the Original Location in FB trials than in the TB trials. In line with this prediction, results showed that a significantly greater proportion of searches in the Original Location Area (bias score of ≥ 9) occurred in the FB trials than in the TB trials. However, because chimpanzees knew that the grape was buried in the New Location, and this knowledge likely inhibited the effect of the belief simulation on their searching behavior, the percentage of subjects (28%) that searched all the way over into the Original Location Area (bias score of ≥ 9) in FB trials was expectedly small. Given the likely inhibitory effect of the knowledge that the grape was buried in the New Location, it is plausible that more of the subjects that were influenced by simulating what the Agent's believed showed a smaller search bias by simply searching closer to the Original Location (rather than all the way into the Original Location Area) in the FB trials than in the TB trials. In line with this prediction, a higher percentage of subjects showed a greater bias in the direction of the Original Location in FB trials than in TB trials (60%) than did not (40%), and the median bias score for the entire group was marginally significantly higher in FB trials than in TB trials. While this effect of the continuous bias measure is in the direction predicted by the simulation model, it is only marginally significant with a small effect size. Thus, the results of this continuous measure of bias should be interpreted cautiously.

A limitation of our study is that subjects are given only one of each experimental trial (FB and TB trial), preventing an assessment of subjects' response patterns over repeated experimental trials. However, giving repeated experimental trials could have created the greater problem of preventing subjects from predicting the Agent's search behavior in subsequent experimental trials. It is critical to our test of the simulation model that subjects are presented with a reliable signal that cues them to anticipate that the Agent will search in the trough in the experimental trials. We used the trough's movement toward the Agent in the experimental trials as such a signal. In the warm-up trials, the trough's movement toward the Agent reliably indicates that the Agent will search in the trough for the grape. However, because the Agent does not search in the trough in the experimental trials, we were concerned that giving repeated experimental trials in which the Agent does not search in the trough after the trough is moved toward the Agent would prevent subjects in subsequent experimental trials from predicting that the Agent will search in the trough. Thus, given that we were analyzing group effects, not individual performance, we chose to limit the experimental trials to avoid this potential problem.

Recently, Heyes (2014) argued that results from change-of-location false belief tests can be more parsimoniously explained by subjects' susceptibility to retroactive interference (RI), a disruption of memory for event X because it is followed by a "perceptually salient" event Y (p. 141). On an RI explanation of our results, it may be hypothesized that the Agent's return to the trough in the FB trial is a perceptually salient event that disrupted the chimpanzees' memory that the grape was buried in the New Location, leaving them with the earlier memory that the grape was buried in the Original Location. The earlier memory would then lead the chimpanzees to search for the grape in the Original Location Area in the FB trial but not in the TB trial.

Previous change-of-location studies, however, have shown that chimpanzees and other apes are not susceptible to RI when an experimenter returns to the testing area. In a visible-displacement task in Call and Tomasello (1999), apes watched, along with an experimenter, while one of two containers was baited with food. While the experimenter's back was turned, the apes watched the food moved from the first container to the second container. The experimenter then turned forward again, and the apes were allowed to select a container. In the RI hypothesis, the return of the experimenter (when he/she turned forward again) should have caused the apes to forget that the second container was baited and left them with the memory that only the first container had been baited, resulting in their preferential selection of the first (unbaited) container. What the researchers found, however, was that apes selected the baited container at levels significantly greater than chance ($p < .001$), averaging close to 90% correct across the trials. Following the same procedures, Krachun et al. (2009) replicated these findings in a different group of apes. Given these findings, it is unlikely that the returning of the Agent to the trough in our study caused our chimpanzees to forget that the grape was buried in the New Location and to think that it was still buried in the Original Location. Nevertheless, in Experiment 2, we tested the RI hypothesis by running a test similar

to the TB trial in Experiment 1 except that the Agent left and then returned to the trough after the grape was buried in the New Location.

Experiment 2

Method

Participants

Nine adult chimpanzees (*Pan troglodytes*; 24–49 years old; average age 30; 5 males, 4 females) from the Yerkes National Primate Research Center (YNPRC) participated in the experiment. Testing was carried out at both the YNPRC's main center in Atlanta, Georgia, U.S.A., and its field station in Lawrenceville, Georgia. All individuals were socially housed in groups ranging from 2–16 individuals in enclosures equipped with indoor/outdoor access, nesting materials, and environmental enrichment items (e.g., toys, swinging and/or climbing structures and barrels). Throughout the study, the chimpanzees were fed their regular diet and had water available *ad libitum*. Chimpanzees were tested individually in their regular indoor or outdoor enclosure. Chimpanzees were not separated from their social group for procedures; rather, experimenters tested individual chimpanzees who were motivated to participate while groupmates were occupied in another area of the enclosure.

Procedure

The same type of trough and substrate (hay) were used as in Experiment 1. The same procedures were used as in Experiment 1 to habituate chimpanzees to the trough and to finding grapes in the hay. Habituation and testing did not occur in a single session and were separated by a minimum of 3 hours. All subjects reached criterion in a single session.

At the beginning of each testing session, the trough with hay was placed approximately 25 cm away from the front of the mesh and at an equal distance between the chimpanzee and the Agent (human experimenter). Immediately preceding the test trial, subjects were given three warm-up trials where they were allowed to find and consume a grape placed or hidden in the center area of the trough. In the first warm-up trial, the grape was placed on top of the hay at the 16.5-inch mark (midpoint between the 8-inch and 25-inch marks on the tape measure). In the second and third warm-up trials, a grape was buried 2.5 inches to the right (19-inch mark) or the left (14-inch mark) of the midpoint. The order of right and left burials was counterbalanced across subjects. Immediately following the last warm-up trial, the chimpanzee watched the Agent bury a grape at the Original Location. The chimpanzee then watched the Agent dig up the grape and rebury it at the New Location. As in Experiment 1, the Original and New Locations were at the 8-inch or 25-inch mark and counterbalanced across subjects. Each time, the Agent buried the grape approximately 2 cm deep in the hay so that it could not be seen. The Agent left the area after burying the grape in the New Location and returned 1 minute later. Upon his/her return, the Agent moved the trough toward the mesh, allowing the chimpanzee to dig up and consume the grape. Thus, the test trial was similar to the TB trial in Experiment 1 except that the Agent left and then returned to the trough after the grape was buried in the New Location. Each subject received one testing session, consisting of three warm-up trials and one test trial.

Coding

The same coding and analyses were used as in Experiment 1. The video recordings of all nine experimental trials—one trial for each subject—were analyzed by one primary coder (RL). An independent coder who was naïve to all test conditions was instructed to view the screen shots and determine, in ½-inch increments, the location of the finger(s) crossing the tape measure. Interrater reliability was assessed by

Spearman correlation. The results show near-perfect interrater reliability ($r = 1.00$, $p < .001$), with just one disagreement in one trial of a half inch.

Results

Eight chimpanzees searched in the New Location Area, and only one chimpanzee searched in the Original Location Area (see Table 2 in Appendix). This preference for selecting the New Location Area was significant in an exact McNemar's test ($N = 9$, $p = .020$, one-tailed, effect size = 9/1 or 9). All statistical analyses for Experiment 2 were run on SPSS, version 27.

Discussion

The purpose of Experiment 2 was not to provide data on search bias to compare with Experiment 1; rather, it was to provide an independent test of the RI hypothesis that the return of an experimenter is a perceptually salient event that causes retroactive inference in chimpanzees. In Experiment 2, the experimenter moved the grape from the Original Location to the New Location while the chimpanzee watched, left the testing area, returned after 1 minute, and moved the trough toward the chimpanzee to search for the grape. According to the RI hypothesis, the experimenter's return is expected to disrupt the chimpanzees' memory that the grape was buried in the New Location, leaving them with the earlier memory that the grape was buried in the Original Location. Contrary to what would be expected on the RI hypothesis, a significant number of searches (8/9) occurred in the New Location Area, indicating that the return of the experimenter did not cause the chimpanzees to forget that the grape was buried in the New Location. Given the results of our control test, plus the results of previous change-of-location tests with chimpanzees and great apes, it is highly unlikely that the biasing effects observed in our study were due to our chimpanzees' susceptibility to retroactive interference effects on memory in change-of-location tests.

General Discussion

Apes have shown that they are able to predict that other agents will search for objects of interest where the agents have evidence to believe the objects are hidden (Buttelmann et al., 2017; Kano et al., 2019; Krupenye et al., 2016; Schmelz et al., 2011; Schmelz et al., 2012). The metarepresentation model explains these findings in terms of the apes representing that other agents have beliefs about the location of objects and predicting that others will search for objects where they believe them to be hidden. The simpler simulation model explains these findings in terms of the apes simulating believing what others believe about the location of hidden objects and predicting that others will behave as they (the apes) imagine behaving while simulating these beliefs. Simulating believing what others believe about the environment is hypothesized to involve first-order representations about the environment that are similar in content to first-order representations that encode one's own beliefs about the environment such that both types of representations are predicted to have similar effects on one's own behavior toward the environment (see Gallese & Goldman, 1998; Goldman & Jordan, 2013; Gordon, 1986). Thus, the simulation model predicts that apes should show a signature altercentric effect in their search behavior in a change-of-location false-belief test. We tested this prediction by giving chimpanzees a change-of-location false-belief test and measured where they searched for a grape that they saw moved from one location (Original Location) to another (New Location). The simulation model predicts that simulating believing what the Agent falsely believes about the location of the grape should influence the chimpanzees to behave as if they shared the false belief of the Agent, resulting in significantly more searches in the Original Location Area in the FB trials than in the TB trials. The results of our study confirmed this prediction. Also, in line with the simulation model, a higher percentage of subjects showed a greater search bias in the direction of the Original Location in FB trials than in TB trials (60%) than did not (40%). Furthermore, the difference in bias scores across conditions was marginally significant. The combination of these results suggest that some

chimpanzees are highly influenced in their search behavior by others' false beliefs about the location of food, while the majority of chimpanzees show less robust signs of search bias.

It has been suggested that the findings from recent change-of-location false-belief tests with apes (Buttelmann et al., 2017; Kano et al., 2019; Krupenye et al., 2016) can be more parsimoniously explained on a submentalizing model (Heyes, 2017) or on a metarepresentation model in which apes are taken to attribute perceptual states but not beliefs (Tomasello, 2019). Results from a recent control study (Kano et al., 2017; Krupenye et al., 2017) have ruled out the submentalizing model as a plausible account of how apes successfully predict the behavior of other agents in change-of-location false-belief tests. However, the perception-attribution model remains a plausible alternative explanation of the findings from these studies. According to the perception-attribution model, apes metarepresent other agents' perceptual states (e.g., states of seeing) and predict that other agents will search for objects of interests in locations where the agents last saw the objects hidden (Tomasello, 2019). It could be hypothesized that the chimpanzees in our study used the perception-attribution process, rather than a simulation process, to predict that the Agent will search for the grape in the Original Location in the FB trials.

Although the results of our study are consistent with the perception-attribution model, the model itself does not predict the results. There is nothing in the perception-attribution model, any more so than in the metarepresentation model that takes apes to attribute beliefs, that predicts that apes should show signs of sharing the false beliefs of other agents whose behavior they are predicting; nor are there any studies (save the present one) that show that apes actually do show signs of sharing the false beliefs of other agents whose behavior they are predicting. The simulation model, on the other hand, predicts the findings of our study. The simulation model also offers a simpler explanation of our findings *and* the findings of the recent change-of-location false-beliefs tests, as the perception-attribution model credit apes with sophisticated metarepresentational abilities (the ability to attribute perceptual states) that the simulation model does not. In addition, the perception-attribution model cannot explain the findings from Schmelz et al.'s (2011, 2012) studies, while the simulation model can. In both studies, Schmelz and colleagues found that chimpanzees predict that another agent (chimpanzee) will search in locations where the agent is presented with evidence about where food is hidden, even though the agent never saw food placed in those locations. In Schmelz et al. (2011), the evidence of the location of hidden food was a slanted board that suggested the food was hidden underneath it; and in Schmelz et al. (2012), the evidence was a photo of food placed on the front of a container that suggested that the container had food inside. Because the competitors never saw food placed in either location, chimpanzees could not have predicted where the agents would search “on the basis of visual or auditory perception” (Schmelz et al., 2011, p. 3077). In contrast, chimpanzee could have predicted where the agents would search (e.g., behind the slanted board) by simulating believing what the agent believed when the agent was presented with the evidence (slanted board) of where the food was hidden. Thus, the simulation model provides not just a simpler but a more unified account than the perception-attribution model of the various findings from recent ToM studies with apes. For these reasons, we argue that the simulation model provides a more plausible account of the data from our study and the data from recent ToM studies with apes than the perception-attribution model.

It is important to note here as well that nothing in our study rules out the possibility that apes employ a mixed model – simulation *plus* metarepresentation – to predict others' behavior. It has been suggested by Kamps et al. (2015), for example, that human infants use their own first-order belief system to encode the contents of others' first-order beliefs—what we call simulation—as a first step in forming metarepresentations about the beliefs of other agents. On a mixed model, then, apes are taken to predict others' behavior on ToM tests (e.g., change-of-location false-belief tests) by forming metarepresentations about others' beliefs, which they do by first simulating, in their own first-order belief system, the contents of others' beliefs. The data from our study do not exclude the possibility that simulation processes provide the basis for metarepresentational capacities that apes may or may not have. Thus, a mixed model explanation is consistent with our data and the data from the other ToM studies with apes. However, a mixed model is strikingly more complex than the simulation model, as it credits apes with metarepresentational capacities that the simulation model does not. For this reason, we take the mixed

model as providing a less plausible explanation of the data from our study than the explanation provided by the simulation model.

Over the years, various behavior-rule explanations have been given for the results of ToM studies with great apes (Povinelli & Vonk, 2003). It might be thought, therefore, that a behavior-rule explanation could be given for the search bias data in our study. Because the last place the Agent in our study looks is different in the FB and TB trials, it might be suggested that the search bias data from our study merely show that chimpanzees simply learned during the study, or know in advance, the rule to search for hidden food in locations where they have seen another agent last looking. This behavior-rule hypothesis is certainly consistent with our data and should be given serious consideration. Future research is needed in order to fully evaluate the plausibility of this hypothesis. However, pending such future research, we believe there are, at present, two reasons to take this behavior-rule interpretation of the search bias results of our study to be less plausible than the simulation model's interpretation.

First, results from Study 1 (subject-first condition) of Kaminski et al. (2008) show that chimpanzees do *not* have a tendency to search for hidden food where they have seen another agent last looking. Before describing the study, it is important to note that Kaminski et al.'s Study 1 (subject-first condition) is not a change-of-location false belief test, and so the simulation model does not predict a search bias from the subjects in the study. The simulation model, as noted earlier, only predicts a search bias in situations in which the subject has a simulated belief about where an object is located that *conflicts* with the subject's own true belief about where the object is located, and that sort of conflict only arises in change-of-location false belief tests. In Study 1 (subject-first condition) of Kaminski et al. (2008), a chimpanzee subject and another agent (a second chimpanzee) watch while food is hidden under a container. During the baiting process, the subject chimpanzee can see the other agent looking at the food and the container while the food is being hidden under the container. Next, only the subject is allowed to see that a second container is also baited with food. Thus, both containers at this point have food inside them, and the subject knows this. After the baiting of the second container, the subject is allowed to select one of the containers. In this test, unlike change-of-location false belief tests, the first container remains baited, which means the other agent's belief that this container is baited remains true. Again, since the other agent does not have a false belief about where food is hidden, the simulation model does not predict that chimpanzees will show a search bias for the container that the agent falsely believes contains food. However, if the behavior-rule hypothesis that chimpanzees tend to search for hidden food in locations where they have seen another agent last looking is true, then we would expect the chimpanzees in Kaminski et al.'s Study 1 (subject-first condition) to show a preference for the first container (where the agent last looked). Contrary to what the behavior-rule hypothesis predicts, subjects did not select the first container at levels above chance. Thus, the results of Kaminski et al.'s Study 1 (subject-first condition) do not support the behavior-rule hypothesis that chimpanzees tend to search for hidden food in locations where they have seen another agent last looking. Second, it is also unlikely that our chimpanzees, in the warm-up trials, could have learned the behavior rule to search in locations where the Agent last looked. Call and Tomasello (1999) tried to teach great apes a very similar behavior rule. In their pretest control, apes were given a choice of two containers in which to search for food. The baited container was always the container on which an experimenter placed and removed a marker, and, as a result, it was the container at which the experimenter had last looked. It took the apes on average 60 trials to learn the rule to select the baited container. The chimpanzees in our study had a total of 6 warm-up trials (3 in the FB session and 3 in the TB session) in which they were allowed to search for food. It is unlikely that our chimpanzees might have learned to follow the behavior rule to search in locations where the Agent last looked, given that it took Call and Tomasello's apes approximately 10 times as many trials to learn a nearly identical behavior rule. Although these previous data make it unlikely that our results are due to chimpanzees simply searching in locations where they saw the Agent last looking, we acknowledge that the search bias results of our study are, in principle, open to a behavior-rule interpretation and should be interpreted cautiously.

It is unknown to what degree simulation processes in chimpanzees are modulated by the social identity and nature of other agents. Empathy studies have shown that human subjects are more likely to show signs of sharing the emotions of other agents the more the other agents are viewed as similar to the

simulator and the less they are viewed as competitors (Lee et al., 2018; Singer et al., 2006). A similar form of modulation may apply to acts of simulating what others believe in chimpanzees. It is also unknown whether simulating believing what others believe has an adaptive function other than the prediction of others' behavior. It is possible that simulation also functions to enable effective coordinated behavior in complex social groups. It is also possible that simulation may function as a method for vicarious learning about the environment. Simulating believing what others believe when others believe that an object or animal is dangerous or important, for example, may serve to bias simulators to act with caution or interest toward such objects and animals. Further research is needed to determine to what degree the social identity and agonistic level of other agents modulates the biasing effects of simulation in chimpanzees, as well as whether simulation has adaptive functions in addition to predicting the behavior of others.

Recent studies have shown that human cognition and behavior are profoundly altercentric (Kampis and Southgate, 2020; Southgate, 2019). In a variety of contexts, our egocentric responses to the physical environment are influenced not only by the non-social facts around us but also by the social facts around us concerning what others are perceiving and thinking. Simulation has been suggested as a plausible explanation for some of these altercentric effects involved in perspective-taking (Frischen et al., 2009; Ward et al., 2020; Ward et al., 2019). Particularly relevant here, however, are recent findings from change-of-location false-belief studies showing that the false beliefs of others appear to influence subjects to behave as if they shared those false beliefs (Bardi et al., 2017; Deschrijver et al., 2016; Kaddouri et al., 2020; Kovács et al., 2010; Kovács et al., 2014; Nijhof et al., 2017). The results of our current study provide suggestive evidence that chimpanzees also show such altercentric effects in a change-of-location false belief task. Young children, like chimpanzees, have also been shown to predict what others will do in similar false-belief tasks (Buttelmann et al., 2009; Southgate et al., 2007). The simulation model provides a coherent and comparatively simple explanation of these findings. According to this model, children and chimpanzees are hypothesized to use a simulation strategy in false-belief contexts to predict what others will do. Humans may be unique, however, in also using metarepresentational strategies to predict others' behavior (Tomasello, 2019; Tomasello & Moll, 2013). Our findings raise the possibility that simulation, given its relative simplicity, may be the evolutionary precursor to metarepresentation in the hominin line.

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Appendix

Table 1

Dataset for Experiment 1

Experiment 1									
Subject	Sex	False-belief trial				True-belief trial			
		Original location	New location	Finger crossing	Bias score	Original location	New location	Finger crossing	Bias score
Adonis	M	25	8	7.5	-0.5	8	25	22.5	2.5
Ajax	M	25	8	7.5	-0.5	25	8	14	6
Allie	F	25	8	13	5	8	25	22	3
April	F	25	8	8	0	25	8	8	0
Bahn	M	8	25	22	3	8	25	25	0
Billy	M	8	25	20.5	4.5	8	25	26	-1
Bo	M	8	25	24.5	0.5	25	8	8	0
Bria	F	8	25	14.5	10.5	25	8	15.5	7.5
Cassie	F	25	8	12	4	25	8	13	5
Catherine	F	8	25	25	0	8	25	25	0
Chinook	M	8	25	12	13	8	25	23	2
Chuhia	F	8	25	14.5	10.5	8	25	17	8
Cordova	M	25	8	8.5	0.5	25	8	8	0
Eesha	F	8	25	26	-1	8	25	20.5	4.5
Ehsto	M	25	8	8.5	0.5	25	8	8	0
Gaygos	M	8	25	24	1	25	8	10	2
Ha'akied	M	8	25	23	2	8	25	19	6
Happy	F	25	8	17.5	9.5	8	25	14.5	10.5
Hug	F	25	8	13	5	25	8	9.5	1.5
Huhkalig	M	8	25	22	3	8	25	18.5	6.5
Idani	F	8	25	4	21	25	8	11.5	3.5
Joey	M	25	8	10	2	8	25	19	6
Kehg	M	25	8	8	0	25	8	23	15
Kia	F	8	25	13.5	11.5	8	25	26	-1
Kudzu	M	8	25	27	-2	25	8	8	0
Kuhta	M	25	8	6.5	-1.5	25	8	5.5	-2.5
Magic	M	25	8	13.5	5.5	8	25	25	0
Maishpa	F	8	25	25	0	25	8	11.5	3.5
Mandy	F	25	8	12.5	4.5	25	8	11	3
Monique	F	8	25	18	7	25	8	11.5	3.5
Nick	M	8	25	20	5	25	8	13.5	5.5
Nowi	M	8	25	1	24	8	25	25	0
Okie	F	8	25	22	3	25	8	10	2
Pepper	F	8	25	13	12	8	25	20	5
Prissy	F	25	8	22	14	25	8	21	13

Punch	M	8	25	16	9	25	8	3.5	-4.5
Quincy	F	8	25	12	13	25	8	11	3
Sabrina	F	25	8	16	8	8	25	23	2
Tabu	M	8	25	25	0	8	25	26	-1
Wotoni	F	8	25	27	-2	8	25	25	0

Note. Bolded numbers are bias scores ≥ 9 , which indicate a bias for searching in the Original Location Area.

Table 2*Dataset for Experiment 2*

Experiment 2					
Subject	Sex	Original location	New location	Finger crossing	Search in New Location Area
Brodie	M	8	25	26	Yes
Carl	M	8	25	14	No
David	M	25	8	15	Yes
Drew	M	25	8	15	Yes
Evelyn	F	25	8	14	Yes
Patrick	M	8	25	24.5	Yes
Rebecca	F	25	8	8	Yes
Sabrina	F	8	25	16.5	Yes
Travis	M	8	25	25	Yes
