

1 Title

2 Great apes use self-experience to anticipate an agent's action in a false belief
3 test

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5 Fumihiro Kano* (1, 2)

6 Christopher Krupenye (3)

7 Satoshi Hirata (1)

8 Masaki Tomonaga (4)

9 Josep Call (3, 5)

10
11 Affiliations:

12 1. Kumamoto Sanctuary, Wildlife Research Center, Kyoto University, Kumamoto, Japan

13 2. Institute for Advanced Study, Kyoto University, Kyoto, Japan

14 3. School of Psychology and Neuroscience, University of St Andrews, St. Andrews, UK

15 4. Primate Research Institute, Kyoto University, Inuyama, Japan

16 5. Max-Planck Institute for Evolutionary Anthropology, Leipzig, Germany

17 *Correspondence: fkanou@gmail.com, Kumamoto Sanctuary, Kyoto University, 990 Misumi, Uki,

18 Kumamoto, 8693201, Japan

19 Abstract (250 words)

20 Human social life depends on theory-of-mind, the ability to attribute mental states to oneself and
21 others. A signature of theory-of-mind, false belief understanding, requires representing others'
22 views of the world, even when they conflict with one's own. After decades of research, it remains
23 controversial whether any nonhuman species possess a theory-of-mind. One challenge to positive
24 evidence of animal theory-of-mind, the behavior-rule account, holds that animals solve such tasks
25 by responding to others' behavioral cues rather than their mental states. We distinguish these
26 hypotheses by implementing a version of the "goggles" test, which asks whether, in the absence of
27 any additional behavioral cues, animals can use their own self experience of a novel barrier being
28 translucent or opaque to determine whether another agent can see through the same barrier. We
29 incorporated this paradigm into an established anticipatory-looking false belief test for great apes.
30 In a between-subjects design, apes experienced a novel barrier as either translucent or opaque,
31 though both looked identical from afar. While being eye-tracked, all apes then watched a video in
32 which an actor saw an object hidden under one box. The actor then scuttled behind the novel
33 barrier, at which point the object was removed. Only apes who experienced the barrier as opaque
34 visually anticipated that the actor would mistakenly search for the object in its previous location.
35 Apes therefore appeared to attribute differential visual access based specifically on their own past
36 perceptual experience to anticipate an agent's actions in a false belief test.

37 Keywords: Anticipatory-looking, Behavior-rule, Goggles test, Nonhuman animals, Theory-of-mind

38 **Significance (120 words)**

39 Many unique features of human communication, cooperation, and culture depend on theory-of-
40 mind, the ability to attribute mental states to oneself and others. But is theory-of-mind uniquely
41 human? Nonhuman animals, like humans' closest ape relatives, have succeeded in some theory-of-
42 mind tasks; however, it remains disputed whether they do so by reading others' minds or their
43 behavior. Here we challenged this behavior-rule account using a version of the "goggles" test,
44 incorporated into an established anticipatory-looking false belief task with apes. We provide
45 evidence that, in the absence of behavioral cues, apes consulted their own past experience of seeing
46 or not seeing through a novel barrier to determine whether an actor could see through the same
47 barrier.

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50 In a seminal article entitled “Does the chimpanzee have a theory of mind?”, Premack and Woodruff
51 (1) defined theory-of-mind as the ability to impute unobservable mental states to oneself and others.
52 After decades of research, it remains controversial whether theory-of-mind is uniquely human (2,
53 3). Particularly central to this debate is the question of whether any nonhuman animals exhibit false-
54 belief understanding, the hallmark of a representational theory-of-mind. False belief understanding
55 reflects awareness that others’ behavior is driven not by reality but by beliefs about reality—and
56 that those beliefs may differ from one’s own.

57 Call and Tomasello (2) argued that chimpanzees do indeed possess a theory-of-mind—as
58 evidenced by convergent performance on diverse social cognitive experiments—but that they likely
59 lack its richest signature, an understanding of others’ false beliefs. More recently, however, great
60 apes (chimpanzees, bonobos, and orangutans) have passed several false belief tests (4, 5), adapted
61 from minimally demanding paradigms originally developed for human infants (6-8). For example,
62 Krupenye, Kano, et al. (4) developed an anticipatory-looking test (based on 6) in which apes watched
63 videos while their gaze was non-invasively eye-tracked. In the videos, an actor looked on as an
64 object was hidden in one of two locations but the object was subsequently moved or removed while
65 the actor was away. As the actor approached centrally toward the two locations, in anticipation of
66 his search for the hidden object, apes looked to the location where the actor falsely believed the
67 object to be, even though they knew it was no longer there. The experimental design controlled for
68 several lower-level explanations and a subsequent control experiment ensured that apes were not
69 simply responding to domain-general cues (9-11). These results are consistent with the possibility
70 that apes anticipated the actor’s action by tracking his beliefs about the object’s location.

71 However, they are also open to the possibility that apes relied on a behavior-rule, innate or
72 learned, that agents tend to search for things where they last saw them (4, 12, 13). Similar behavior-

73 rule or behavior-abstraction accounts have been levied against findings from human infants (7, 13,
74 14) as well as the entire corpus of theory-of-mind research in nonhuman animals (3, 15, 16).
75 Despite the development of numerous elegant paradigms, in most instances, participants have
76 access to some behavioral cues that may permit them to correctly anticipate an actor's behavior
77 without inferring the content of her mind.

78 Heyes (15) proposed an experimental design (inspired by Novey (17) and several other
79 researchers), later known as the “goggles” test, to distinguish mind-reading from alternatives such
80 as behavior-reading. The key question is whether a participant can use her own past experience of
81 visual access through novel goggles to determine whether others can see through the same goggles;
82 in other words, whether she understands others not based on observable behavioral cues but rather
83 by projecting her own mental state onto them. Meltzoff and Brooks (18) first successfully
84 implemented this manipulation with young human children in a gaze-following test. More recently,
85 Senju, Southgate, Snape, Leonard and Csibra (19) integrated this manipulation into an anticipatory-
86 looking false belief test (6): two groups of 18-month-old infants first experienced either an opaque
87 blindfold or a trick blindfold that looked identical but could be seen through. While being eye-
88 tracked, both groups subsequently watched the same video sequence in which an actor saw an
89 object be hidden in one location and then put on a blindfold before the object was removed. The
90 children who had worn the opaque blindfold—but not those who had worn the trick blindfold—
91 treated the actor as though she had a false belief: they looked in anticipation of her searching for the
92 object in its previous location.

93 Chimpanzees have also been tested on several versions of the goggles task. They failed to
94 preferentially beg for food from, or to gaze-follow, a human experimenter wearing a see-through
95 visor or mask as compared with an experimenter wearing an opaque one (16, 20). However, in a

96 food-competition test, chimpanzees correctly attempted to steal a competitor's food from behind an
97 opaque screen as compared with a screen that appeared identical but that the chimpanzees had
98 previously seen through (20). This last result suggested that apes can pass the "goggles" test and
99 represent what others can see, at least in certain context where apes show enhanced motivations to
100 solve the task (21, 22).

101 The present study tested whether great apes pass a "goggles" version of an anticipatory-
102 looking test modelled on previous tests with great apes and human infants (4, 6, 19). Apes first
103 experienced seeing or not seeing through an identical novel barrier (a between-subject design).
104 Then, while being eye-tracked, they all watched the same video in which a human actor first saw an
105 object hidden in one location. The actor then moved behind the novel barrier before the object was
106 shifted and then removed. If apes can use self-experience to infer the actor's perspective, those who
107 experienced the barrier as translucent should attribute a true belief to the actor but those who
108 experienced the barrier as opaque should instead attribute a false belief. Accordingly, we predicted
109 that only the apes in the opaque condition should look in anticipation of the actor searching for the
110 object in its original location. Critically, the original anticipatory-looking tasks involved two
111 matched conditions, FB1 and FB2 (4, 6). In FB1, the actor watched an object be hidden in one
112 location and moved to a second, and then was absent when the object was ultimately removed. In
113 FB2, the actor watched the object be hidden in one location and then was absent when the object
114 was moved to the second and ultimately removed. Although Senju et al. used the FB1 design of
115 Southgate et al., we decided to instead use the FB2 design because recent attempts to replicate
116 Southgate et al. with human populations found greater difficulty replicating the FB2 design (23-26).
117 We thus thought that the FB2 design would constitute a more stringent test of action anticipation in
118 apes.

119

120 Method

121 Participants

122 Forty-seven great apes (29 chimpanzees, *Pan troglodytes*, 14 bonobos, *Pan paniscus*, 4 orangutans,
123 *Pongo abelii*; from Kumamoto Sanctuary, Kumamoto, Japan, Primate Research Institute, Inuyama,
124 Japan, and Leipzig Zoo, Leipzig, Germany) were randomly assigned to either the opaque (n = 23)
125 or see-through (n = 24) condition (between-subjects). Two additional apes (1 chimpanzee and 1
126 orangutan) participated in the familiarization trial but refused to approach the test setup on the
127 following day, and thus could not be included in the test trial. We initially considered testing apes
128 on a within-subject design and, consequently, all Kumamoto apes first experienced a test trial
129 involving black barriers (translucent and opaque properties counterbalanced across individuals) in
130 real life and in video followed by a second trial with white barriers (on a separate day). However,
131 we noticed a few problems with the black barrier (one of the chimpanzees was afraid of this barrier,
132 and the translucent version was more difficult to see-through than its white counterpart). Therefore,
133 in proceeding with the experiment, we instead used white barriers only (in real life and in video) for
134 all other apes. Because we wanted to ensure that apes were responding to identical actions in the
135 videos, we analyzed the data from the white barrier conditions alone (i.e., trial 2 for Kumamoto
136 apes, trial 1 for all other apes). We confirmed that performance of the Kumamoto apes, who had
137 experienced the additional black barrier, did not differ significantly from that of the other apes (see
138 SI for this analysis). Most apes had participated in the original study (4) approximately three years
139 earlier; however, false belief trials always ended before the actor searched in either location and
140 thus did not provide experience about how individuals with false beliefs behave. See Table S1 for
141 the details about each participant.

142 Apparatus

143 Eye-tracking was performed with great apes following an established procedure (27). Apes' eyes
144 were recorded by an infrared head-free eye-tracker (60 Hz; X120 in Leipzig and X300 in Japan;
145 Tobii Technology AB, Stockholm, Sweden). The eye-tracker and monitor were installed outside of
146 the testing room. Apes were allowed to sip juice via a custom-made dispenser (irrespective of their
147 gaze behavior) and to watch videos presented through a transparent panel. The videos were
148 presented with a resolution of 1280×720 pixels at a viewing distance of 70 cm on a 23-inch LCD
149 monitor (43×24 degree) with Tobii Studio software (version 3.2.1). Two-point automated
150 calibration was conducted for each ape by presenting a small object or video clip on each reference
151 point. We then assessed the quality of calibrations by visually checking the calibration results
152 indicated in the software after the calibration, and also checking whether the ape's gaze point was
153 not substantially deviated from a small reference icon presented before each recording session. We
154 repeated the calibration procedure whenever necessary. Calibration errors in apes are typically
155 within a degree, following these procedures (27).

156 Stimuli and Procedure

157 The procedure consisted of presentation of a familiarization video, self-experience of an opaque or
158 translucent barrier in real life, and presentation of the test video. Videos largely followed the design
159 of the FB2 condition of study 2 of Krupenye, Kano et al (4). As in that study, we maximized apes'
160 engagement by embedding false belief manipulations within agonistic conflicts between an ape-like
161 character (Kong) and a human actor (Actor). On the first day, apes watched a pair of familiarization
162 trials, identically designed to those used in Krupenye, Kano et al (Experiment 2). In the first
163 familiarization trial, Kong hid an object in one of two identical boxes in front of Actor. Actor
164 attempted to obtain the object by reaching ambiguously toward the two boxes, finally overturning

165 the correct box and grasping the object. The second familiarization was identical, except the object
166 was hidden in, and retrieved from, the other box. The purpose of the familiarization trial was to
167 demonstrate that the object could be hidden in either box, and that Actor would search for it after
168 witnessing its hiding. The familiarization trials were presented one day before the test trials,
169 following the original study with apes (4) unlike studies involving human infants (6, 19). We made
170 this decision to minimize the duration of a video presented each day and thereby ensure apes'
171 attention to the video throughout. A previous study confirmed that apes can remember video events
172 across consecutive days (28).

173 After watching the familiarization video, we introduced apes to either an opaque or see-
174 through barrier in real-life (on the same day for Leipzig and Inuyama apes but the next day for
175 Kumamoto apes; Figure 1 and Fig. S2). Both barriers consisted of a wheeled frame (80 cm in width
176 * 160 cm in height) covered with white fabric. For the see-through barrier, several layers of white
177 mesh cloth were used. For the opaque barrier, a similar looking but opaque white mesh-like cloth
178 was used. All materials were novel to the apes. Both barriers were decorated with shiny red and
179 green tinsel to be distinguishable from any other normal barrier. The see-through barrier was
180 translucent and could be seen through at a close distance, but both barriers appeared identical from
181 afar (e.g. the distance of the barrier in the test video). During the self-experience phase, an
182 experimenter brought either barrier into the room, and positioned it in front of the ape
183 (approximately 1-2 m from the ape; Movie S1). The experimenter then ostensibly presented
184 various objects and food beside, and then behind, the barrier, demonstrating its occlusive property.
185 In each facility, the same experimenter performed the same actions across the conditions. During
186 the presentation of an object/food, the experimenter ensured 1) that the ape was attending to the
187 object before moving it behind the barrier (and called the ape's name or changed the object if not)

188 and 2) that the trajectories of the object and the experimenter's hand (and gaze) were identical
189 across conditions. This self-experience phase lasted for approximately 5 minutes.

190 The test trial occurred on the following day (i.e., day 2 for Leipzig and Inuyama apes and
191 day 3 for Kumamoto apes). On the test day, apes again experienced a 1-2 minute self-experience
192 reminder phase. The barrier was removed from the room and then, while being eye-tracked, the
193 apes watched the test video, which did not differ between conditions (Figure 1; also see Movie S1).
194 The test events did not differ from those in the Krupenye, Kano et al (4) study except that Actor's
195 perceptual access was manipulated, not by leaving thorough the door, but by hiding behind the
196 barrier. In the test video, Actor first brought the barrier (which appeared opaque at this distance)
197 into the scene. Kong then appeared and hid the object in one of the two boxes while Actor watched
198 (Figure 1a). Actor then scuttled behind the barrier with legs visible below, to ensure that apes
199 tracked his presence (Figure 1b). Kong then removed the object from the box (Target), relocated it
200 to the other box (Distractor), retrieved it once more and left the scene (Figure 1c). Actor then
201 returned from behind the barrier, and attempted to obtain the object by reaching ambiguously
202 toward the two boxes (Figure 1d). This middle-reach lasted for 6 sec. We counterbalanced across
203 participants as evenly as possible the locations where the object was hidden in the familiarization (L
204 then R vs R then L), as well as the locations where the object was last hidden in the test (L or R);
205 i.e. four combinations: LRL, LRR, RLL, and RLR).

206 To assay apes' anticipations about where the actor would search, during the 6-seconds of
207 the actor's ambiguous middle-reach, we coded to which box each ape looked first as well as each
208 ape's Differential Looking Score (DLS; total viewing times to Target minus total viewing times to
209 Distractor, divided by the sum of these values). First looks and viewing times were automatically
210 calculated in Tobii Studio based on pre-defined areas of interest (Fig. S1). The seminal study by

211 Southgate, Senju and Csibra (6) used both first look and DLS measures, although more recent
212 studies have focused primarily on DLS because this measure appears to show more consistent
213 patterns (24, 29, 30). If apes can use their own past experience to determine an agent's mental state,
214 we predicted that their patterns of anticipatory looking should differ between conditions;
215 specifically, their looking should be more biased toward the Target than Distractor (accordant with
216 attribution of a false belief) in the opaque condition than in the see-through condition (where they
217 should instead attribute a true belief), and they should show above chance looking toward the
218 Target in the opaque condition only.

219 Results

220 Apes did not differentiate between conditions in their first looks to Target vs. Distractor (Table 1; P
221 = 0.46, Fisher's exact test). However, as predicted, their DLS was significantly more biased toward
222 the Target in the opaque condition than in the see-through condition (Figure 2; Wilcoxon rank sum
223 test, $Z = 2.13$, $N = 30$, $P = 0.033$, $r = 0.39$). DLS was also significantly higher than chance (i.e.,
224 biased toward the Target; Wilcoxon signed rank test, $Z = 2.35$, $N = 13$, $P = 0.019$, $r = 0.65$) in the
225 opaque condition, but at chance level in the see-through condition ($Z = 0.80$, $N = 17$, $P = 0.42$, $r =$
226 0.19).

227 Moreover, no significant difference was detected between species in either the opaque
228 condition (Kruskal-Wallis rank sum test, $\chi^2(2) = 0.81$, $P = 0.66$) or the see-through condition ($\chi^2(2)$
229 = 2.06, $P = 0.35$). The opaque condition was akin to a replication of the FB2 condition of the
230 Krupenye, Kano et al (4) study. To test this with an independent sample of apes, we reanalyzed the
231 data from the opaque condition, excluding the 3 ape participants from this condition who had
232 previously been tested in the FB2 condition of that study (i.e., all apes included in this analysis
233 either had not participated in that study or had been tested in the FB1 condition). DLS remained

234 significantly above chance (0.52 mean \pm 0.66 95%CI, $Z = 2.15$, $N = 11$, $P = 0.032$, $r = 0.60$),
235 consistent with the DLS data from the FB2 condition in Krupenye, Kano et al (0.65 mean \pm 0.38
236 95%CI, $Z = 2.94$, $N = 12$, $P = 0.0033$, $r = 0.82$).

237

238 Discussion

239 Our results suggest that apes used their own past perceptual experiences to determine an agent's
240 perceptual access and anticipate how the agent would behave. Apes who had experienced the
241 barrier as opaque treated the actor as not having seen the object's movement and removal, and as
242 having a false belief that the object remained in its original location: they showed a bias in looking
243 toward the location the object originally inhabited, consistent with anticipation that the actor would
244 search for the object there. Apes who had experienced the barrier as translucent showed no such
245 bias, consistent with attributing to the actor a true belief that the object had been removed and with
246 having no expectation that the actor would search in any particular place.

247 Despite viewing identical familiarization and test events, apes' looking behavior differed
248 between conditions. Critically, apes had never witnessed any other agents interacting with the novel
249 barriers, precluding reliance on an abstraction or rule about how others behave in this novel context.
250 Their differences in looking, which accord with attribution of true versus false beliefs, therefore
251 derive specifically from their differential perceptual experience of these novel barriers. Our results
252 thus support the theory-of-mind account.

253 Heyes (31) summarized several alternatives in response to Senju and colleague's (19)
254 related findings with human infants. Heyes questioned whether "the opaque group did, and the trick
255 group did not, discriminate between the boxes on test because the infants in the trick group were
256 less distracted by the blindfold, and therefore were more likely themselves to see removal of the toy
257 (object) from the scene during the belief induction trial." However, in this study, by measuring
258 apes' looking times to the barrier and boxes at each event in the video sequence, we confirmed that
259 apes' attention to the object displacement events did not differ between conditions—nor did their
260 attention to the barrier at any particular event (Fig. S3). Heyes also proposed that human infants

261 might have perceived similarities between the cloth materials used for the blindfolds and the
262 common cloth materials used in households. This concern does not apply to our study because we
263 selected cloth materials that were not usually seen in our facilities. Finally, Heyes questioned
264 whether participants could perceive any differences in actions performed by the experimenter
265 during familiarization of the opaque and see-through barriers. To prevent this possibility, we
266 ensured that the same experimenters performed the same actions across conditions.

267 Although the “goggles” test is seen as a method for distinguishing the theory-of-mind
268 account from non-mentalistic alternatives (15), the paradigm has received some philosophical
269 scrutiny (e.g. 12, 32, 33). Specifically, the theory-of-mind account proposes that, in this paradigm,
270 participants experience “seeing” or “not seeing” through a barrier as an unobservable mental state
271 and attribute that same inner experience to the agent behind the barrier. Non-mentalistic accounts
272 generally conceive of “seeing” in behavioral terms: as there being an unobstructed line of sight
273 between an agent and an object (32). In principle, participants could solve the goggles task in a non-
274 mentalistic way if, in the self-experience phase, they are simply learning whether the barrier
275 obstructs a line of sight and, in the test, applying existing rules or abstractions about how agents
276 usually behave around barriers that do or don’t obstruct line of sight (12). Thus, the behavior-rule
277 previously applied to other false-belief tests – ‘agents tend to search for things where they last saw
278 them’ (13) could be modified as ‘agents tend to search for things in the last location where they
279 established a line of sight unobstructed by a learnt property of a barrier’. At a minimum, however,
280 as Meltzoff and Brooks (18) argued, participants are “learning a psychological affordance, not a
281 simple physical or motor affordance—and moreover are learning how it affects the self and
282 applying it to others”. Importantly, the original behavior-rule account –that agents search for things
283 where they last saw them (13) – cannot be applied in any straightforward manner to this or Senju

284 and colleagues' (19) study because, across conditions, apes and infants generate different
285 anticipations in response to an identical set of actions.

286 If our current results are not explained by behavior rules, do they constitute evidence of
287 full-brown false-belief understanding? Apperly and Butterfill (34, 35) have argued, for example,
288 that humans are endowed with such a minimal mindreading system from infancy, allowing for
289 efficient but inflexible anticipation of behavior through tracking of belief-like states, and that
290 human adults have a second cognitively effortful system for flexibly representing propositional
291 attitudes. The minimal system can represent encountering (i.e., that an object has been within an
292 agent's visual field) and registering (i.e., it can represent the last place the agent encountered the
293 object, even if the object has been moved after the agent departed the scene). Minimal mind-readers
294 can therefore track belief-like states that are akin to beliefs about an object's location. Accordingly,
295 they can accurately anticipate an agent's action in change-of-location false belief tasks, the
296 paradigms most commonly used in research with human infants and nonhuman animals. Critically,
297 the signature limit of such a minimal system is its inability to track genuine beliefs about object
298 identity (36, 37). Testing this limitation in the future will be important for precisely specifying the
299 representational mechanisms underlying action anticipation in both human and nonhuman primates.

300 Our results derive from the Differential Looking Score (DLS) rather than apes' first-looks
301 (where no clear effects were obtained). This mosaic of results is consistent with several other
302 anticipatory-looking studies with human participants in which DLS also provided more consistent
303 findings than first looks, and may emerge from common elements of many anticipatory looking
304 paradigms (29, 30). DLS derive from a longer time window (6 seconds in this study), presumably
305 providing more time for participants to generate their anticipations and potentially making them
306 more robust to noise. Because looking can be sensitive to perceptual and cognitive influences

307 beyond action anticipation, it is likely that the strength of first look versus DLS measures will vary
308 between individual paradigms. Importantly, our DLS results are consistent with similar work in 18-
309 month-old humans (19), and they replicate previous findings with great apes (4).

310 Recent replication attempts for the Southgate-Senju paradigm were successful overall in
311 replicating the FB1 design, but not the FB2 design, with both human adults and infants (for a
312 summary and commentary, see 24). It is therefore important to highlight that this study replicated
313 our previous DLS findings in nonhuman apes, specifically from the FB2 design (4). Although it
314 remains unclear which factors impact replicability with human participants, researchers have
315 proposed that several procedural differences between studies may be responsible (24). Of special
316 note, one interesting result from previous replication studies is that, while some researchers found a
317 chance-level effect for FB2 (26), others found a below-chance effect for FB2 (as well as an above-
318 chance effect for FB1) in the Differential Looking Scores (23, 25). One interpretation for this
319 puzzling pattern is that human participants showed a location bias: they may have simply looked at
320 the last location that the object inhabited (before it was finally removed). Interestingly, in previous
321 anticipatory-looking studies that adopted similar designs for apes and human infants, human infants
322 anticipatorily looked at the location where a target object was before its relocation (in an inanimate
323 control condition (38)), while apes did not show the same position bias (39). The reason for this
324 potential species difference is unknown but could be related to a species difference in general eye-
325 movement properties; specifically, that the ape eye is less likely than the human eye to be locked in
326 a certain fixation location (27). Most relevantly here, replication of FB2 with nonhuman apes
327 supports the general validity of the Southgate-Senju design, at least for certain population/species.
328 However, to increase the utility of this paradigm, future studies should identify which aspects of the
329 procedure are likely to cause replication failures (or position biases) in human participants. In
330 addition, as Southgate (in 24) pointed out, it is likely critical that researchers ensure that participants

331 are “highly engaged by the agent’s actions, so that they are entirely focused on predicting what she
332 will do next” in an anticipatory-looking test. As we have shown here, the use of dramatic stories
333 optimized for the target age/species may be one way to achieve more reliable gaze-based measures
334 of action anticipation (40).

335 In conclusion, we provide evidence that great apes can use their own past experience of
336 visual access to attribute perception and, potentially, resultant beliefs to others. Our results are
337 consistent with findings from 18-month-old humans (19). Notably, they are also consistent with
338 findings from corvids showing that they use their own visual and pilfering experiences to guard
339 their caches against pilferers in a food competition task (41, 42). These results together corroborate
340 the idea that young infants and nonhuman animals have a theory-of-mind, and do not simply rely on
341 behavior rules to interpret and anticipate others’ actions. They also highlight the important role that
342 self-experience may play in expanding the states of mind that infants and animals can attribute to
343 others (43). However, additional tests are necessary to further rule out non-mentalistic alternatives.
344 Particularly in the case of this study, rather than attributing their own inner experience to the actor,
345 it is possible that apes learned about the psychological affordances of the barriers and used this
346 information to determine whether the actor had an unobstructed line of sight (but see 44 for a recent
347 evidence against this possibility in a different research paradigm). Moreover, to determine whether
348 apes represent agents’ beliefs or belief-like states, it will be necessary to investigate their ability to
349 anticipate an agent’s action based on false beliefs about object identity. At a minimum, the present
350 study has shown that, in the absence of any differential behavioral cues during the test, apes make
351 different anticipations of an agent’s actions depending on their own past experiences of perceptual
352 access. Our findings therefore contest the straightforward conception of the behavior-rule account.

353

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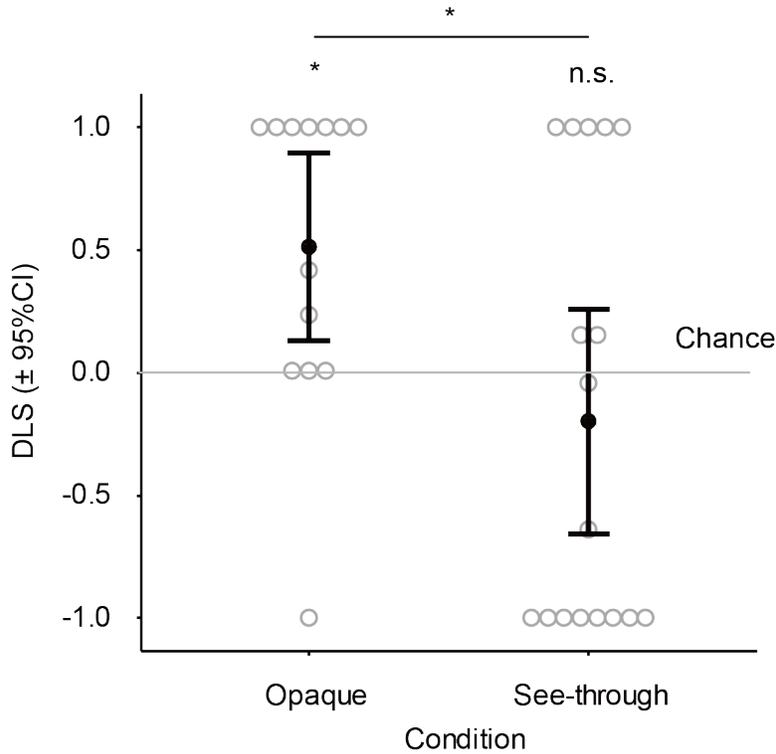
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458

459 Figure 1. The test video sequence used in this study (See Movie S1). (a) Actor watches Kong hide
 460 an object in the left (Target) box. (b) Actor scuttles behind barrier. (c) Kong moves object to right
 461 (Distractor) box and then removes object. (d) Actor reaches ambiguously toward boxes. If apes who
 462 experienced the barrier as opaque attributed no visual access (and a false belief that the object
 463 remained in the Target location) to Actor, their looking in anticipation of the actor's search should
 464 be biased toward the Target box. Conversely, if those who experienced the barrier as see-through
 465 attributed a true belief to Actor (that the object had been removed), their looking should be at
 466 chance, consistent with no prediction.



467

468 Figure 2. Differential Looking Score (\pm 95% confidence intervals; calculated as looking to Target
 469 minus looking to Distractor divided by the sum of these values; i.e. positive DLS indicates looking
 470 bias toward Target) as Actor reached ambiguously toward the Target and Distractor boxes in the
 471 opaque and see-through conditions. The Target is the location where the Actor last saw the object
 472 before moving behind the barrier. Thirteen and 17 apes looked at the boxes during the ambiguous
 473 reach, in the opaque and see-through conditions respectively, while the rest did not look at either
 474 (i.e. no DLS data). The chance level is zero. Dots indicate participants' individual data. Asterisks
 475 indicate $P < 0.05$ in nonparametric tests.

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