

1 Title (up to 8 words)

2 Primates pass dynamically social anticipatory-looking false belief tests

3  
4 Authors (up to 3)

5 Fumihiro Kano (1)

6 Josep Call (2)

7 Christopher Krupenye (2, 3)

8  
9 Affiliations:

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

11 2. School of Psychology and Neuroscience, University of St Andrews, St. Andrews, UK

12 3. Department of Psychological & Brain Sciences, Johns Hopkins University, Baltimore, MD,

13 21218, USA

14  
15 Correspondences: [fkanou@gmail.com](mailto:fkanou@gmail.com) (F. Kano), [ckrupenye@gmail.com](mailto:ckrupenye@gmail.com) (C. Krupenye)

16  
17 Keywords: comparative cognition, apes and monkeys, theory of mind, mental state attribution, social  
18 cognition, eye-tracking

19

20

21 Main text (up to 800 words)

22 Three recent studies have shown that nonhuman apes and macaques pass anticipatory-looking (AL)  
23 false-belief (FB) tests [1-3], inspired by seminal work with humans [e.g. 4]. These results raise the  
24 possibility that both apes and monkeys understand that others' actions are driven not by reality but by  
25 beliefs about reality, even when those beliefs are false. In response, Horschler, MacLean, and Santos  
26 [5] argued that these findings 'should be interpreted cautiously due to methodological and theoretical  
27 challenges paralleling trends in the human literature.' We agree that continued work is necessary to  
28 identify factors that influence reproducibility of AL paradigms, and also to specify the mechanisms  
29 and functions of the observed behaviors in primates. However, inferences from the human literature  
30 (summarized in [5]) should be made with caution because key nonhuman results have largely been  
31 replicated and extended across different groups and species [1-3], so far providing a different picture  
32 from more variably replicable human studies. Moreover, nonhuman studies retain only the conceptual  
33 design of human paradigms with various improvements and optimization for nonhuman primates (Box  
34 1). What we see as the more pressing—but potentially interwoven—matter is resolving discrepancies  
35 among comparative findings: apes and monkeys have passed AL-FB tests (visually anticipating that  
36 an agent would search for an object where she falsely believed it to be) but monkeys have not  
37 succeeded in violation-of-expectation (VoE) FB paradigms [e.g. 6] (they do not look longer when an  
38 agent's search is inconsistent with her FBs). Below, we spotlight crucial methodological differences  
39 that may explain the unique success of nonhuman AL paradigms. In concluding, we discuss adaptive  
40 significance and future directions.

41 Departing from most human AL paradigms and from nonhuman VoE studies, nonhuman AL  
42 tasks have embedded FB content within dynamic social interactions with intuitive action goals (e.g.,  
43 agent seeks a competitor or contested object). Stimuli were crafted to motivate social primates to  
44 closely track agents' interactions and understand agents' goals. Agents' approach or reaching actions  
45 were designed to appear natural and goal-directed, to evoke spontaneous anticipatory-looking to  
46 proximal action targets. Notably, in the absence of such dynamic social stimuli, apes do not reliably  
47 anticipate agents' actions [7, 8] (but see diverse stimuli in [3]). Moreover, among the most replicable

48 human AL studies are those that promote understanding and action-anticipation through verbal story-  
49 telling and anticipation-prompting questions [9]. We suggest that nonverbal equivalents, such as  
50 familiar stories and anticipation-prompting scene configurations (e.g. Tom-and-Jerry, Y-shaped tunnel;  
51 [10]) accomplish the same. Including these elements in nonhuman VoE studies may also improve  
52 performance. Working in free-ranging settings, nonhuman VoE studies have employed relatively  
53 simplistic live-acted events, but high rates of distraction may indicate shallower engagement with  
54 these stimuli. Although these paradigms have demonstrated standard true-belief (TB) phenomena, it  
55 is possible that only the most engaging and motivating stimuli can reveal primates' (including  
56 humans') full range of capacities.

57 VoE and AL both offer powerful and complementary nonverbal methods for tapping, under  
58 minimal task demands, what we suspect are largely the same socio-cognitive phenomena. However,  
59 procedural differences also exist: whereas VoE uses general, reactive metrics (attention to displayed  
60 outcomes), AL uses specific, proactive ones (anticipatory gaze to action targets). AL tasks often  
61 remove the goal object before the agent seeks it, reducing cognitive demands while precluding a reality  
62 bias. Proactive/targeted looks and object removal also control for the possibility that participants  
63 expect random error or uncertainty from the agent by attributing ignorance rather than belief.  
64 Accordingly, AL uses two FB conditions to prompt distinct patterns of anticipation, akin to VoE TB-  
65 FB designs (but note TB-FB comparisons: [2]). It remains an open question whether these procedural  
66 differences influenced nonhuman findings.

67 Importantly, AL but not VoE allows direct observation of online action anticipation, which  
68 hints at inherent functional advantage in social interaction. Relatedly, we think it unlikely that primates'  
69 FB-related capacities are entirely implicit (lacking expression beyond eye-movements). Actionable  
70 FB understanding may have been obscured by the repeated use of a single context (food-competition)  
71 in previous ape studies [11], where FB-consistent performance could not be dissociated from  
72 knowledge-ignorance interpretations. Note that departure from that paradigm has provided evidence  
73 for such dissociation in an action-based task [12]. Critically, to date, researchers have been unable to  
74 test FB understanding in other fitness-relevant contexts (e.g., severe aggression, mating, infant

75 survival) because they are challenging to capture experimentally (although AL allows closer  
76 reproduction of some related contexts). Yet, it might be in those scenarios – confronting agents  
77 engaged in risky social interactions with important fitness consequences – that FB understanding is  
78 most reliably expressed. Future work must further explore action-based, VoE, and AL paradigms, the  
79 design and contextual factors that shape performance and replicability, and the mechanisms by which  
80 primates pass FB tests. Only with this combination of efforts—and careful experimental control of  
81 competing influences on behavior (including gaze)—will we be able to fully characterize the  
82 representations and processes that support primate social cognition.

83

#### 84 Acknowledgement

85 We thank Isao Hasegawa, Daniel Horschler, Evan MacLean, and Matthias Allritz for constructive  
86 comments.

87

88 Box 1. Methodological differences between nonhuman and human AL-FB studies

89 Nonhuman AL-FB studies were optimized for nonhuman primates, and improved based on criticism  
90 of original human AL designs, by 1) counterbalancing the side in which key events occurred during  
91 familiarization and test [1-3]; 2) adopting multi-scenario/trial designs to stabilize within-individual  
92 response variation [1, 3] (note that comparing individual differences across studies is therefore more  
93 meaningful than doing so within studies); 3) using short movies involving dynamic social interactions  
94 [1-3] and a training procedure [3] to maintain attention and engagement; 4) using familiar props (e.g.  
95 haystack, metal mesh, stone, door) and intuitive scenarios to aid nonhuman participants' understanding  
96 of characters' actions and goals [1-3]; 5) presenting natural reaching and approach scenes that evoke  
97 anticipatory looking to proximal targets; and 6) using challenging conditions (e.g., FB2) with fewer  
98 low-level explanations in all tests [1-3]. It remains untested whether some of these changes could  
99 improve replicability in human AL-FB studies. Moreover, some parameters, such as optimal analysis  
100 windows of anticipatory looks (first looks and total looking duration), could be further evaluated in  
101 future human and nonhuman AL-FB tasks—although this should be optimized in each task, rather  
102 than simply standardized across tasks, because cognitive demands vary across tasks (e.g. [1, 2]).

103

104 References (up to 12)

105 1. Krupenye, C. et al. (2016) Great apes anticipate that other individuals will act according to  
106 false beliefs. *Science* 354 (6308), 110-114.

107 2. Kano, F. et al. (2019) Great apes use self-experience to anticipate an agent's action in a false-  
108 belief test. *Proc Nat Acad Sci* 116 (42), 20904-20909.

109 3. Hayashi, T. et al. (2020) Macaques exhibit implicit gaze bias anticipating others' false-belief-  
110 driven actions via medial prefrontal cortex. *Cell Reports* 30 (13), 4433-4444.e5.

111 4. Southgate, V. et al. (2007) Action anticipation through attribution of false belief by 2-year-olds.  
112 *Psychol Sci* 18 (7), 587-592.

113 5. Horschler, D.J. et al. (2020, in press) Do non-human primates really represent others' beliefs?

- 114 Trends Cogn Sci.
- 115 6. Martcorena, D.C.W. et al. (2011) Monkeys represent others' knowledge but not their beliefs.
- 116 Dev Sci 14 (6), 1406-1416.
- 117 7. Krupenye, C. et al. (2017) A test of the submentalizing hypothesis: Apes' performance in a false
- 118 belief task inanimate control. Communicative & Integrative Biology 10 (4), e1343771.
- 119 8. Kano, F. et al. (2017) Eye tracking uncovered great apes' ability to anticipate that other
- 120 individuals will act according to false beliefs. Communicative & Integrative Biology 10 (2),
- 121 e1299836.
- 122 9. Clements, W.A. and Perner, J. (1994) Implicit understanding of belief. Cogn Dev 9 (4), 377-
- 123 395.
- 124 10. Meristo, M. et al. (2016) Early conversational environment enables spontaneous belief
- 125 attribution in deaf children. Cognition 157, 139-145.
- 126 11. Call, J. and Tomasello, M. (2008) Does the chimpanzee have a theory of mind? 30 years later.
- 127 Trends Cogn Sci 12 (5), 187-192.
- 128 12. Buttelmann, D. et al. (2017) Great apes distinguish true from false beliefs in an interactive
- 129 helping task. PLoS One 12 (4), e0173793.
- 130