Title (up to 8 words)

Primates pass dynamically social anticipatory-looking false belief tests

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Main text (up to 800 words)

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

Departing from most human AL paradigms and from nonhuman VoE studies, nonhuman AL tasks have embedded FB content within dynamic social interactions with intuitive action goals (e.g., agent seeks a competitor or contested object). Stimuli were crafted to motivate social primates to closely track agents' interactions and understand agents' goals. Agents' approach or reaching actions were designed to appear natural and goal-directed, to evoke spontaneous anticipatory-looking to proximal action targets. Notably, in the absence of such dynamic social stimuli, apes do not reliably 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

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

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

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

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