likely that primates' FB-related capacities are entirely implicit (lacking expression beyond eye movements). Actionable FB understanding may have been obscured by the repeated use of a single context (food competition) in previous ape studies [11], where FB-consistent performance could not be dissociated from knowledge–ignorance interpretations. Note that departure from that paradigm has provided evidence for such dissociation in an action-based task [12]. Critically, to date, researchers have been unable to 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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Letter

Advancing Gaze-Based Research on Primate Theory of Mind

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In Horschler et al. [1], we reviewed three new anticipatory looking (AL) studies of false belief (FB) representation in non-human primates (hereafter primates) [2–4] in relation to similar studies in humans [5]. We concluded that AL evidence of belief representation in primates should be interpreted cautiously due to challenges shared with the human literature, as well as a large body of work previously suggesting that primates do not represent others' beliefs. In response, Kano, Call, and Krupenye [6] argue that comparative AL studies have been more replicable in primates than in humans, that resolving discrepant findings between AL and violation of expectation (VoE) paradigms should be prioritized, and that issues related to ecological validity may partially explain the lack of evidence for belief representation in previous comparative work. In this article, we address these three points, ultimately emphasizing our agreement on the powerful potential of gaze-based measures in theory of mind research.

First, Kano et al. [6] argue that unlike similar human studies [5], comparative results 'have largely been replicated and extended across different groups and species', potentially due to differences in methodology and stimuli. Although we acknowledge the important design differences the authors discuss (e.g., dynamic stimuli emphasizing social competition in comparative studies), we disagree that these results show greater replicability. As reviewed in [1], the three comparative studies to date [2–4] employed a variety of dependent measures and response time-windows. These different dependent measures (e.g., first look vs. differential looking score) in varying time-windows, and even identical measures across theoretically identical experiments, produced conflicting findings in these studies [2–4]. Similar patterns are evident across many human AL studies, suggesting that strong conclusions about positive results should be reserved until a clearer picture of which procedural variants are most reliable, replicable, and internally valid emerges [1]. It is also noteworthy that, as in the human literature, most comparative AL (and VoE) studies are carried out by only a handful of laboratories. Thus, future replication attempts from a greater number of research groups will aid procedural refinement, similar to ongoing efforts in the human literature.

Second, Kano et al. [6] argue that discrepancies between findings from AL and VoE paradigms (e.g., [7]) present a more pressing issue, and we agree that addressing these discrepancies is an important aim for future research. Kano and colleagues suggest that the use of dynamic social stimuli in comparative AL studies may account for the observed differences. In contrast to this claim, the one comparative AL study that used both dynamic social stimuli and traditional stimuli more similar to VoE studies found that subjects were more likely to show FB-congruent looking patterns when traditional stimuli were used [4]. We argued instead that AL and VoE findings may differ in part because of specific study design features that have made it difficult for AL studies to directly compare analogous true belief (TB), FB, and ignorance conditions (Box 1). Despite these caveats, we agree that work employing AL and VoE measures in identical study designs, with both apes and monkeys, will be fruitful in addressing these issues.

Third, Kano et al. [6] argue that previous comparative FB tests failed to show positive results in part because they focused on food competition contexts, whereas other fitness-relevant contexts (e.g., mating and aggressive encounters) remained unexplored. They note that 'it might be in those scenarios – confronting agents engaged in risky social interactions with important fitness consequences – that FB understanding is most reliably expressed'. We agree that ecological validity is a critical issue, and that incorporating greater contextual diversity may provide important insights. However, comparative AL paradigms are entirely virtual with no reward at stake, whereas previous explicit tasks failing to demonstrate FB representation have involved actual competition with live conspecifics, and real potential for injury or loss of resources (e.g., subordinate and dominant chimpanzees with conflicting beliefs about the location of hidden food competing directly [8,9]). Indeed, many scholars have emphasized the ecological validity of these very tasks [10] relative to previous paradigms that lacked direct competition and required extensive training [11,12]. If primates do represent others' beliefs, it is puzzling to us that they show no strong evidence of doing so in food competition contexts that closely mimic fitness-relevant situations in the wild.

Despite our differing perspectives, we fully agree with Kano and colleagues that future work incorporating diverse gaze-based measures across a range of ecologically relevant conditions will be critical in resolving these issues. As nonverbal measures, these approaches have great potential for probing the representations that guide social behavior in both preverbal humans and other animals, enabling direct comparisons across species. We look forward to the continued development of this work and the insights it will provide about the evolution of theory of mind.

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Box 1. Study Design Differences Between AL and VoE Tasks

Kano et al. [6] note that 'AL uses two FB conditions to prompt distinct patterns of anticipation, akin to VoE TB-FB designs'. These two FB conditions control for ignorance attribution and reality biases by removing the object from the scene before the test. However, these conditions are not akin to VoE TB-FB designs. In comparative VoE studies (e.g., [7]), the object has always remained in a hiding location rather than being removed completely. In this way, subjects are expected to make positive predictions about the location an agent will act on in both TB and FB conditions in VoE studies. By contrast, in AL TB conditions [3], because the object is removed, agents only have a TB that the object is gone (but not about where it is). Subjects cannot form a clear prediction about what the agent will do next based on this TB. Therefore, VoE but not AL studies have tested cases where an agent is expected to make a specific action based on a TB in direct comparison to a FB. Future AL work should employ designs that can dissociate positive predictions in TB and FB conditions from those in which an agent is completely ignorant.

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