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Spotlight

Belief Representation in Great Apes

Alia Martin*

A new study by Kano and colleagues shows that great apes use their own visual experience to attribute perceptions and beliefs to another agent. Their results suggest that the way apes understand behavior is more similar to human understanding than was previously thought, and may be driven by representations of mental states.

What cognitive mechanisms underlie primate theory of mind? Psychologists disagree about the answer to this question, but until recently they often agreed about the pattern of results their theories needed to explain: non-human primates showed a sophisticated ability to track the current or past perceptual access of other agents, but showed no evidence of representing false beliefs [1].

This pattern has been upended by a groundbreaking new experiment. Kano and colleagues [2] demonstrate that great apes anticipate the actions of an agent with a false belief [3], and that their ability to do so is not dependent on learned rules about how others behave. Apes can apply their own experience to make inferences about what another agent can see, and what that agent will therefore believe.

Kano *et al.* showed 49 apes – chimpanzees, bonobos, and orangutans – videos of agonistic interactions between a human actor and 'Kong', an ape-like character. Two introductory videos established the setup: Kong hid an object in one of two boxes while the actor watched, and the actor then retrieved it. Next, apes were given 5 minutes of live experience with one of two possible barriers. From afar, the barriers looked identical, but on close inspection, one was made of see-through mesh, whereas the other was completely opaque.

The next day, apes were shown the test video. The actor watched as Kong hid the object in a box (box A). The actor then hid behind a barrier that resembled the one the apes had experienced, while Kong moved the object into the other box (box B). Finally, Kong removed the object from the scene, and the actor returned. The researchers recorded the gaze direction of the apes using an eye tracker to measure whether they anticipated which of the boxes the actor would search.

Apes who had experienced the opaque barrier spent more time looking at box A, suggesting that they thought the actor falsely believed that the object was still there. By contrast, apes who had experienced the see-through barrier showed no looking bias, suggesting that they understood that the actor knew, correctly, that the object had been removed. The only difference between these conditions was apes' experience with the barrier itself, and therefore they must have applied their own experience of the properties of the barrier to reason about the actor: there were no differences between the videos shown in each condition.

These findings are striking. Only 5 minutes of real-life experience with the transparent barrier influenced the predictions apes made about the behavior of another agent – an agent of a different species, seen on a video screen, a day later. The results suggest that apes are capable of tracking beliefs, and not merely by using learned cues of visual access. Although the barrier in the video always appeared opaque, those apes who believed it was in fact see-through (based on their experience with a transparent mesh barrier) did not focus on the box where they had last seen the actor looking at the object.

The findings of Kano *et al.* conflict with theories arguing that non-human primates use learned rules to understand behavior [4], or only track awareness or knowledge (but not beliefs) [1,5]. These accounts predict that apes should not be able to use their own experience to make belief-based predictions. However, that is exactly what these apes do. We might now wonder whether great apes are unique among non-human animals in their ability to track perception and belief, or whether new implicit tests will reveal similar evidence in other primates like macaques, and in other socially sophisticated species such as corvids. Moreover, given that human infants have shown an ability to attribute beliefs in the same task [6], what might this tell us about shared mindreading systems between infants and apes? (Box 1).

If ape mindreading is more similar to human mindreading than was previously thought, an intriguing possibility raised by these findings is that apes might be inadvertently influenced by the beliefs of others in the same

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Box 1. An Efficient System, or an Efficient Learning System?

Could the performance of apes in the experiments of Kano *et al.* be the work of a limited but efficient mindreading capacity, similar to the idea of core knowledge? Such theories argue for innate, phylogenetically ancient, domain-specific capacities, with signature limits on their inputs and computational capacity [9]. The efficient mindreading system is thought to be distinct from, and maintained alongside, the flexible mindreading system that is the hallmark of adult social reasoning [10].

However, the findings of Kano *et al.* suggest that ape mindreading has an impressive flexibility. Its inputs are not fixed to canonical cues of perceptual access; instead, two identical events are interpreted differently depending only on what apes know about the perceptual affordances of the barrier. This type of top-down modulation of system inputs, and equivalency between own-experience and other-experience, suggest that ape mindreading is not tied to innately specified cues. One possible interpretation of these findings is thus that apes do possess the same efficient mindreading system as human infants, but that in humans, via learning and coordination with other species-unique capacities, this system develops into our flexible adult theory of mind [11]. Designing studies to further examine these alternatives is an exciting avenue for comparative and developmental psychologists.

way as humans are. Human adults [7] and infants [8] experience spontaneous interference from the beliefs of other agents. Perhaps apes also experience this type of interference in the task designed by Kano *et al.* – believing, in the opaque condition, that the object is in fact where the actor last saw it. Testing whether apes can recall the true location of an object, after inferring the false belief of another agent, will shed light on whether apes can simultaneously hold dual conflicting representations, and clarify the extent to which apes resemble humans in their susceptibility to mental influence.

The findings of Kano *et al.* raise further tantalizing questions about how the apes' construal of the barrier changes once they discover its transparent property. Do apes who have experienced a transparent barrier subsequently attribute to the actor a true belief that the object is no longer in the scene? Or does the barrier reduce their certainty that the actor should have a false belief, leading them to treat him as simply ignorant? One exciting possibility is that apes may actually recognize a causal connection between perceptual access, the experience of seeing, and the formation of a belief. Once exposed to a transparent barrier, might apes be able to make reverse inferences about the perceptual affordances of a barrier based on the searching behavior of an agent? For instance, if an agent occluded by a barrier searches correctly for an object, perhaps apes would be more interested in inspecting the barrier to see whether its opaque appearance is deceptive (how else could the agent know where the object is?). Finally, perhaps apes might recognize that other apes would still expect the barrier to be opaque, and could use this information to their advantage in competition (e.g., if a banana were available behind the seemingly opaque barrier).

Irrespective of the answers to these questions, the clever methods that Kano *et al.* have introduced will help to advance our understanding of the mechanisms underlying many aspects of mindreading in great apes.

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Spotlight

Exercise, Dopamine, and Cognition in Older Age

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Jonasson *et al.* investigated whether individual differences in human dopamine receptors (D2R) were related to cognitive performance before and after a 6-month aerobic exercise intervention (compared with active control). While D2R decreased (perhaps counterintuitively) with exercise, there was no relationship between D2R and working memory at baseline or following exercise.