

Eye-tracking as a window into primate social cognition

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Abstract

Over the past decade, noninvasive, restraint-free eye-tracking research with primates has transformed our understanding of primate social cognition. The use of this technology with many primate species allows for the exploration and comparison of how these species attend to and understand social agents and interactions. The ability to compare and contrast the cognitive capacities of various primate species, including humans, provides insight into the evolutionary mechanisms and selective pressures that have likely shaped social cognition in similar and divergent ways across the primate order. In this review, we begin by discussing noninvasive behavioral methods used to measure primate gaze and attention before the introduction of noninvasive, restraint-free eye-tracking methodologies. Next, we focus on findings from recent eye-tracking research on primate social cognition, beginning with simple visual and search mechanisms. We then discuss the results that have built on this basic understanding of how primates view images and videos, exploring discrimination and knowledge of social agents, following social cues, tracking perspectives and predicting behavior, and the combination of eye-tracking and other behavioral and physiological methods. Finally, we discuss some future directions of noninvasive eye-tracking research on primate social cognition and current eye-tracking work-in-progress that builds on these previous studies, investigating underexplored socio-cognitive capacities and utilizing new methodologies.

KEYWORDS

comparative cognition, great apes, monkeys, noninvasive eye-tracking, primates

1 | INTRODUCTION

Primates have generally evolved to live in complex social groups, and humans especially are said to be “ultra-social” (Boyd, 2006; Boyd & Richerson, 1996; Herrmann et al., 2007). We use sophisticated cognitive abilities (the brain's capabilities to process, store, and retrieve information) for navigating our complicated social environments, mechanisms that provide the foundation for uniquely human

traits like cumulative culture and language, and that have facilitated the spread of human populations across every continent (Bayne et al., 2019; Henrich, 2017; Herrmann et al., 2007; Shettleworth, 2009; Tomasello, 2009). Research on social cognition (i.e., the cognitive mechanisms used to navigate one's social environment) in primates is vital for comprehending the selective pressures that drove the evolution of this multifaceted sociality (Humphrey, 1976). Comparing and contrasting the socio-cognitive abilities of humans with other

Abbreviations: cm, centimeter; ToM, theory of mind.

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primates provides insight into the evolutionary trajectory of these cognitive mechanisms across the primate order, from simple recognition of and discrimination between unique individuals to more complex abilities like reading the minds of others (Tomasello & Call, 1997; Whiten & Erdal, 2012). Scientists have long used behavioral methods to investigate and compare socio-cognitive capacities across primates and humans. However, new insights have been enabled thanks to the adaptation of eye-tracking for restraint-free, noninvasive use with nonhuman primates (Hopper et al., 2021). This technology has allowed us to measure the eye movements of primates to make important discoveries about how they attend to and process the visual world around them.

All mammals, including primates, have evolved the capacity to control their eye movements (Walls, 1962). Eye movements are used to shift gaze, which here we define as the target of an individual's attention. Eye movements include fixations (continuous attention to one target), voluntary saccades (gaze shifts from one location to another), and smooth pursuit (eyes remaining fixated on a moving object). This flexible system of attention allows animals to attend to the most salient and important stimuli in their environments (Land, 1999; Schumann et al., 2008). Animals' eye movements and attentional patterns vary widely depending on the nature of the environment, stimulus, and/or task, and this variation can reveal important information about the cognitive processes, both conscious and unconscious, that drive these eye movements (Yarbus, 1967). Eye-tracking technology, originally developed for use with humans, has recently been utilized to study the cognitive processes and resulting eye movements of nonhuman animals (Hopper et al., 2021). This technology has enabled scientists to move beyond purely behavioral measures of fixation times measured by hand using video recordings, and allows for more in-depth measurements of fixation patterns, saccades, attentional biases, loss of visual acuity, and changes in pupil dilation (Hopper et al., 2021).

1.1 | Overview of eye-tracking research with nonhuman primates

Eye-tracking is possible with a number of nonhuman species but there has been particular interest in its use with nonhuman primates (hereafter referred to as primates). As our closest living relatives—and with similar physiology—comparative research with primates is capable of identifying shared behavioral and psychological traits that likely evolved millions of years ago in a common ancestor, thus enabling a deeper understanding of the evolutionary trajectory of human cognition (Tomasello & Call, 1997). This review aims to describe the multitude of ways in which noninvasive eye-tracking can be useful for research on primate social cognition. We also summarize the recent advances and scientific contributions that have resulted from eye-tracking experiments with nonhuman primates. Here we focus on primate eye-tracking research with an emphasis on noninvasive and restraint-free methods.

Invasive and restraint methodologies for measuring eye-movement patterns in primates, including the use of surgical implants and head/chair restraints, are common in some fields. These techniques enable precise quantification of the target of attention, but they have major welfare costs and preclude research on a range of populations for which invasive research is impossible or deemed unethical. New noninvasive approaches provide the ideal compromise, allowing precise measurement of gaze and pupillary responses in a broad range of taxa under high welfare conditions (Hopper et al., 2021). Noninvasive eye-tracking also permits the presentation of naturalistic or ethologically informed paradigms while retaining a high degree of experimental control (Testard et al., 2021). Thus, while we note that important discoveries about primate social cognition have been made via invasive eye-tracking approaches (e.g., Báez-Mendoza et al., 2021; Deaner et al., 2005; Shepherd, Deaner, & Platt, 2006), the focus of the present review will be on noninvasive experiments.

Noninvasive and restraint-free remote eye-tracking technology with primates improves welfare and permits research on a much greater range of populations (zoo-housed animals, endangered species, direct comparisons with humans, etc.) (Hopper et al., 2021). These innovations have yielded major expansions to our knowledge of primate social cognition. This review will mainly focus on the results from studies using noninvasive and restraint-free eye-tracking technology; first, however, we will briefly review previous noninvasive studies that measured and quantified eye movement patterns using behavioral methods with primates. For a fuller historical description of the early behavioral research on visual attention in primates, see Hopper et al. (2021).

1.2 | Early research on visual attention in primates

The most commonly used nontechnical method for measuring primate attention in recent decades utilizes hand-coding from video recordings of primates' gaze. In these studies, experimenters present subjects with visual stimuli and subjects' gaze and eye movements are video recorded as they view the stimuli. After the test is completed, experimenters use the video recordings to code the duration of subjects' gaze to each stimulus frame-by-frame. This method has been used in lab settings where stimuli are presented either as physical objects or as images on a monitor screen (Dufour et al., 2006; Myowa-Yamakoshi et al., 2003; Neiworth et al., 2006; Pascalis & Bachevalier, 1998; Paukner et al., 2010, 2017; Sclafani et al., 2016; Waitt et al., 2003, 2006). It has also been employed using physical photographs or live displays in studies with free-ranging primates (Anderson et al., 2009; Higham et al., 2011; Hughes & Santos, 2012; Hughes et al., 2015; Martcorena et al., 2011; Simpson et al., 2014). The results from these studies, which have been conducted with multiple primate species including monkeys and apes, have expanded our knowledge about primates' attentional preferences and social and physical cognitive abilities. However, manual coding of videos is labor-intensive, requires ample training to ensure accuracy and reliability, and has more limited temporal and spatial resolution

(Venker et al., 2020). It is also open to experimenter error, as blind coding requires that the target of gaze is not actually included in the video recording (Hopper et al., 2021). For coding coarse measures of attention, manual gaze coding and automatic eye-tracking methods metrics are highly similar, and manual coding can limit data loss. However, eye-tracking has its advantage in reduced manual effort and its delivery of precise information about gaze direction, movement, and pupil size (Venker et al., 2020).

1.3 | Eye-Tracking research with light restraint methods

Some recent eye-tracking studies have used “light restraint” methods, in which primate subjects are lightly held in a stable position in front of the stimuli (Alvarado et al., 2017; Damon et al., 2017; Dettmer et al., 2016; Hirata et al., 2010; Myowa-Yamakoshi et al., 2012; Paukner et al., 2013, 2014, 2018; Simpson, Nicolini, et al., 2016; Simpson, Suomi, et al. 2016; Simpson et al., 2019; Slonecker et al., 2018). Here, “lightly held” means that subjects were either held (infants), positioned in a chair, or voluntarily sat in front of the monitor on which the stimuli was presented, and an experimenter sat next to them in the testing room and lightly positioned their face towards the screen. A second light-restraint method includes training subjects to use a wearable eye-tracker, which is mounted on non-harmful headgear (chimpanzees: Kano & Tomonaga, 2013; ring-tailed lemurs: Shepherd & Platt, 2006). These methods require extensive training and habituation with primate subjects that are not always achievable in zoo or sanctuary settings. Therefore, the majority of this paper will focus on restraint-free eye-tracking with primates as it is the most feasible eye-tracking method for a diverse array of primate species and testing settings.

1.4 | Mechanics of eye-tracking

Noninvasive remote eye-tracking with primates uses an infrared camera (placed a short distance away from the subject) to measure reflections from the cornea to detect subjects' eye movements, positions, and gaze patterns (defined as eye-movement patterns including fixation on a single point and saccades, or shifts in gaze direction; see Hopper et al., 2021 for a full description of the various hardware and software setups used in primate research). In many setups, the eye-tracker is placed below a monitor presenting the stimuli and positioned approximately 60 cm from the subject's face, behind an acrylic or polycarbonate panel (see Figure 1). To capture additional behavior of the subject, a remote video camera may also be mounted on the monitor screen, with both the camera and monitor integrated with the experimenter's laptop to ensure a continuous presentation of stimuli and consistent data processing. Restraint-free methods allow subjects to freely move around the testing enclosure. Various forms of incentives may be used to encourage primate subjects to attend to stimuli and keep their head

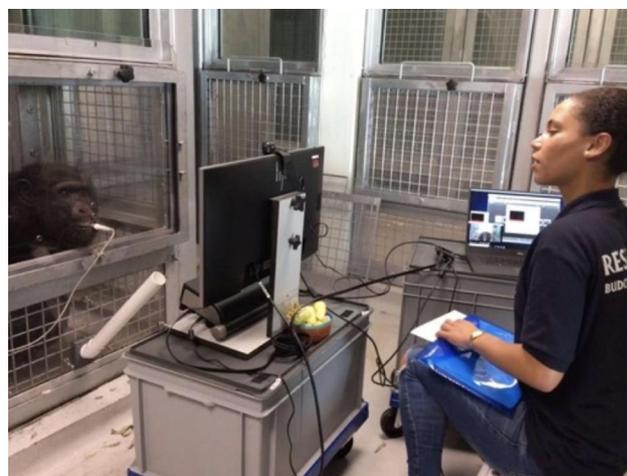


FIGURE 1 Example of restraint-free, noninvasive eye-tracking set up with chimpanzees living at the Edinburgh Zoo, Scotland. The Tobii eye-tracker is placed ~60 cm in front of the subject and directly below the monitor on which stimuli are presented. The voluntary chimpanzee subject is drinking a small amount of diluted juice delivered through a nozzle to help keep them still as they view the stimuli to maximize recording accuracy. The experimenter can simultaneously control stimulus presentation from her laptop and view the subject to ensure they are attending to the stimuli on the screen, which allows for testing to be paused if subjects are no longer attending to trials. Photo courtesy of Kate Grounds.

movements to a minimum to ensure accurate gaze recordings. Most commonly, subjects are given continuous access to a small amount of diluted juice from a nozzle mounted on the transparent panel. Subjects can be calibrated using two or more calibration points, ensuring accurate measurements for each unique subject (see Hopper et al., 2021 for an in-depth description of the various calibration techniques and methods).

Noninvasive restraint-free eye-tracking with primates has transformed our understanding of primate social cognition because of the detailed accuracy with which it captures patterns of attention, gaze, and pupil diameter changes (Hopper et al., 2021). Decoding the social world involves processes of attention that direct our focus to objects and social agents (i.e., individual entities that exhibit goal-directed actions and engage in social behavior) in the environment and parse them from other visual features (Section 2). Recognition and memory for specific agents provides the representational building blocks of the social world, allowing us to build relationships and generate expectations about agents' future actions based on their past behavior (Section 3). Attending to the social cues of these agents (Section 4), like gaze, enhances our ability to predict their behavior and is central to both communication and generation of inferences about their mental states, like goals and beliefs (Section 5). Collectively, these mechanisms permit humans and other primates to track familiar social agents, interpret and predict their behavior, and make decisions about how to behave. Building on foundational insights from traditional nontechnical methodologies, eye-tracking has enabled major advances in our understanding of each of these

fundamental aspects of social cognition. Here, we review results from restraint-free, noninvasive eye-tracking research on primate social cognition (the studies and their findings are also summarized in Table 1), focusing on the major processes and mechanisms outlined in the preceding sentences. We have chosen to summarize the studies organized in these specific sections because they each build on one another in turn, beginning with the most basic aspects of the visual mechanisms that primates use to observe conspecifics, up to some of the most complex cognitive mechanisms that primates may employ to understand and reason about the minds of others. In a final section (Section 6), we review novel eye-tracking applications that deepen understanding of complex social cognitive phenomena by integrating gaze and pupil metrics with other physiological and behavioral techniques. Overall, we hope to highlight both the state-of-the-art on primate social cognition and the unique contributions (and untapped potential) of noninvasive eye-tracking to this important area of research.

2 | FOUNDATIONS OF SOCIAL ATTENTION (VISUAL/SCANNING/SEARCH MECHANISMS)

Eye movement patterns, including scanning mechanisms, fixations, and saccades, reveal a variety of cognitive processes. Both voluntary and involuntary eye movements indicate patterns of visual-spatial attention, sociocognitive processing, and motivational and emotional processing, among other cognitive functions. These flexible eye-movement patterns allow an individual to attend to salient features, both social and nonsocial, in the environment (Schumann et al., 2008). Thus, analyzing an individual's patterns of visual attention can provide insight into the cognitive processes that are driving these patterns.

In addition, living in large and dynamic social groups with complex and differentiated social relationships, as a majority of primate species do, requires an ability to attend to and track different social agents and scenes (Kano & Call, 2017; Lonsdorf et al., 2019; Watts, 1998). Allocating attention to social agents and environments allows individuals to capitalize on mating opportunities, avoid dangerous individuals or interactions, and learn socially from others (Deaner et al., 2005). This first section examines how primates allocate attention to social agents and environments. Although behavioral research has in part helped to answer this question, noninvasive primate eye-tracking research has recently expanded our understanding of how nonhuman primates attend to other individuals and social scenes, by recording not just general direction of attention but rather precise measurement of gaze targets and scan patterns (Hopper et al., 2021).

The first noninvasive eye-tracking study with one of humans' closest relatives, chimpanzees, was published in 2009 by Kano and Tomonaga (2009), and the results were groundbreaking. In it, they compared the gaze of humans and chimpanzees as subjects viewed images of naturalistic scenes of chimpanzees, other mammals, and

humans. The researchers analyzed looking patterns, fixation duration, and sequence of fixations, and found that chimpanzees and humans exhibited remarkable similarities in some of their scanning and gaze patterns but also some important differences. Both species looked for longer durations at the bodies of conspecific and heterospecific agents as compared to the backgrounds in the images, and repeatedly fixated on these informative regions rather than scanning the entire image. However, the chimpanzees made a greater number of fixations that were shorter in duration as compared to humans, and chimpanzees' fixations were more widespread across the image as compared to humans' fixations. When viewing images of chimpanzees and humans both species first looked at the face region, but when viewing images of other mammalian species they viewed the face second, after viewing the body or background. Chimpanzees and humans also looked for a longer duration at the faces of the individuals in all of the images as compared to their bodies. Longer durations of viewing faces across the various image/animal types indicates that both chimpanzees and humans possess a general visual preference for the face. These results were the first to suggest that chimpanzees have active, voluntary control of their gaze, similar to previous results in the human literature (Buswell, 1935; Henderson & Hollingworth, 1999; Yarbus, 1967). However, humans viewed faces for longer durations than did the chimpanzees. The authors note that this may be due to the fact that in nonhuman primates, long fixations on the face of others during social interactions may be a more intense signal of threat as compared to in humans. Generally, these findings imply that humans gain important social information from the faces of others, whereas chimpanzees collect relatively more information from the entire body of other individuals. This first comparative noninvasive eye-tracking experiment with chimpanzees and humans laid the groundwork for further explorations of gaze scanning patterns in nonhuman primate species.

Shortly after this first comparative eye-tracking study with chimpanzees and humans, Kano and Tomonaga (2010) used a similar paradigm to directly compare conspecific and heterospecific face-scanning patterns in chimpanzees and humans (Kano & Tomonaga, 2010). They presented both species with close-up colored photographs of humans, chimpanzees, and nonprimate mammals with either neutral expressions or different forms of emotional expressions. Both humans and chimpanzees exhibited intense scanning of the main facial features when viewing images of chimpanzees and humans, but not other mammals. In addition, both species had the same sequential viewing patterns: they viewed the eyes first and then the mouth region. However, important differences in scanning patterns between the two species were also observed. Humans demonstrated prolonged viewing of the eye regions, while chimpanzees exhibited quick, vertical scanning patterns of the face, with immediate shifts of gaze from the eye to mouth regions. In addition, in response to the faces with different emotional expressions, chimpanzees and humans exhibited divergent scanning patterns. Humans continued to demonstrate prolonged viewing of the eye regions, while chimpanzees demonstrated an increase in viewing of the mouth region when viewing faces with various emotional

TABLE 1 Summary of noninvasive restraint-free eye-tracking research with primates to date, listed in chronological order based on publication date.

Citation	Review section	Short summary of main findings (from abstract)	Species
Kano and Tomonaga (2009)	1 and 3	Chimpanzees and humans both looked at the face region longer than at other parts of the body, and at the animal figures as a whole longer than the background. Chimps shifted their fixations more broadly and more quickly than did humans. Chimps had shorter average fixation durations on the face region than did humans.	<i>Pan troglodytes</i> <i>Homo sapiens</i>
Sliwa et al. (2010, restraint method)	2	Rhesus macaques spontaneously matched the voices of familiar individuals to their faces.	<i>Macaca mulatta</i>
Hattori et al. (2010)	4	Humans were equally sensitive to social cues from conspecifics and chimpanzees, while conspecific social cues modulated chimps' looking behaviors more than human cues. Chimps also looked longer at the conspecific face as compared to the human face.	<i>Pan troglodytes</i> <i>Homo sapiens</i>
Kano and Tomonaga (2010)	1	Chimps and humans first viewed the eye region and then the mouth region. Both species intensely viewed the main facial features like eyes, nose, and mouth. Chimpanzees engaged in quick, vertical scanning over the eye and mouth regions, while humans were more likely to sequentially fixate on the eye region. These species similarities and differences were consistent across conspecific and non-conspecific stimuli.	<i>Pan troglodytes</i> <i>Homo sapiens</i>
Kano and Tomonaga (2011a; Perceptual mechanism)	1	Both humans and chimpanzees used multiple cues to fixate to the face and other socially significant areas. There was no evidence to suggest any differences between the two species in their responses to low-level saliency.	<i>Pan troglodytes</i> <i>Homo sapiens</i>
Kano and Tomonaga (2011b; Species differences)	1	Chimpanzees outperformed humans in their speed of scanning, tracking images at the point of fixation for a longer time than did humans. Chimps also made more fixations per second as compared to humans.	<i>Pan troglodytes</i> <i>Homo sapiens</i>
Kano et al. (2011)	1	In the overlap condition, humans exhibited longer saccade latency as compared to the other great apes. In the gap condition, all species exhibited similar saccade latencies.	<i>Gorilla gorilla</i> <i>Pongo abelii</i> <i>Pan troglodytes</i> <i>Homo sapiens</i>
Kano et al. (2012)	1	While all species predominantly viewed faces and eyes, humans demonstrated prolonged eye viewing as compared to the other apes, independent of eye color. No differences between gorilla and orangutan viewing patterns were detected. The male flange of orangutans affected viewing patterns, while the color contrast of human eyes did not.	<i>Gorilla gorilla</i> <i>Pongo abelii</i> <i>Homo sapiens</i>
Myowa-Yamakoshi et al. (2012)	4	Chimpanzees and humans similarly anticipated action goals, but scan goal-directed actions differently.	<i>Pan troglodytes</i> <i>Homo sapiens</i>
Kano and Call (2014a; Animal Behavior)	4	Each species followed conspecific gaze; while bonobos followed human gaze, chimpanzees did not. Bonobos generally reacted more sensitively to gaze cues as compared to chimpanzees. While bonobos and orangutans followed non-conspecific ape gaze, chimpanzees did not. Human adults followed ape gaze, while human infants did not. Both chimps and human infants exhibited prolonged viewing of conspecific faces.	<i>Pan troglodytes</i> <i>Pongo abelii</i> <i>Pan paniscus</i> <i>Homo sapiens</i>
Kano and Call (2014b; Psych Science)	5	When viewing the claw action, apes did not predictively look at the familiarized goal object rather than the familiarized location. Yet when viewing the hand action, they predictively looked at the familiarized goal object.	<i>Pan paniscus</i> <i>Pan troglodytes</i> <i>Pongo abelii</i>
Kret et al. (2014)	3	Chimpanzees and humans each exhibited enhanced pupil-mimicry when viewing conspecific eyes; effects were strongest in chimp mothers and humans.	<i>Pan troglodytes</i> <i>Homo sapiens</i>

(Continues)

TABLE 1 (Continued)

Citation	Review section	Short summary of main findings (from abstract)	Species
Kano and Hirata (2015)	5	Apes made anticipatory looks toward the object that the human intended to use, rather than the former location of the object.	<i>Pan troglodytes</i> <i>Pan paniscus</i>
Kano et al. (2015)	1	Chimpanzees viewed the mouth, genitals, and target objects longer than did bonobos, while bonobos viewed the face and eyes longer than did chimpanzees.	<i>Pan troglodytes</i> <i>Pan paniscus</i>
Krupenye et al. (2016)	5	Apes looked in anticipation of an agent acting according to his false beliefs, even though apes were aware that the target object was no longer present.	<i>Pan paniscus</i> <i>Pan troglodytes</i> <i>Pongo abelii</i>
Howard et al. (2017)	1	While apes did not demonstrate memory during the non-social condition, they did exhibit memory for the event featuring the social model.	<i>Gorilla gorilla</i> <i>Pan troglodytes</i>
Krupenye et al. (2017)	5	Apes made many fewer anticipatory looks and no significant tendency to look to the correct location in an inanimate control video, despite attending well to key events in the video. Thus, no evidence was found for apes' submentalizing in the false-belief task.	<i>Pan paniscus</i> <i>Pan troglodytes</i> <i>Pongo abelii</i>
Chertoff et al. (2018)	1	Humans focused more on the eyes than did gorillas.	<i>Gorilla gorilla</i> <i>Homo sapiens</i>
Howard et al. (2018)	3	Capuchins remembered events that included a social model significantly more than events that included a nonsocial model.	<i>Sapajus apella</i>
Kano et al. (2018a)	4	In both the ostension and control conditions, chimpanzees followed the actor's gaze to the cued object. Ostensive signals enhanced chimps' attention to the target and distractor objects more strongly than did control attention-getters. This was especially true for chimpanzees who had a close relationship with human caregivers.	<i>Pan troglodytes</i>
Kano et al. (2018b)	1	Within each species, individuals varied in their gaze patterns towards the faces, eyes, mouths, and action targets, dependent on their unique individual experiences.	<i>Pan paniscus</i> <i>Pan troglodytes</i> <i>Pongo abelii</i> <i>Macaca mulatta</i> <i>Homo sapiens</i>
Kano et al. (2019)	5	Apes consulted their past experience of being able to see or not see through a new barrier to determine whether an agent could see through that same barrier in the absence of behavioral cues.	<i>Pan paniscus</i> <i>Pan troglodytes</i> <i>Pongo abelii</i>
Kawaguchi et al. (2019)	2	Chimps viewed infant faces for longer than those of adults when viewing conspecific images, but not when viewing heterospecific images. Bonobos did not view conspecific infant faces for longer than adult faces, and viewed heterospecific adults longer than they viewed heterospecific infants. Chimps did not show any preference when conspecific infant and adult facial coloration was matched.	<i>Pan paniscus</i> <i>Pan troglodytes</i>
Lonsdorf et al. (2019)	2	Males viewed images of males for longer than did females, whereas females viewed images of females for longer than did males. Within each sex, females looked significantly longer at female versus male images; although not significant, males also looked longer at male versus female images.	<i>Sapajus apella</i>
Ryan et al. (2019)	1	Rhesus macaques and titi monkeys viewed videos longer than static images, juveniles viewed stimuli more than monkeys of other age groups, and monkeys' viewing times of stimuli increased across multiple eye-tracking sessions	<i>Macaca mulatta</i> <i>Callicebus cupreus</i>
Sato et al. (2019)	3	Chimpanzees spontaneously attended to injured conspecifics more than non-injured conspecifics, but did not do so in a control condition in which images of injuries were scrambled while maintaining color information. Chimpanzees did not avoid viewing injuries at any point during stimulus presentation. Chimpanzees exhibited a greater nasal temperature reduction in response to injury compared with the control stimulus, indicating arousal.	<i>Pan troglodytes</i>

TABLE 1 (Continued)

Citation	Review section	Short summary of main findings (from abstract)	Species
Wolf and Tomasello (2019)	2	Great apes who have visually attended to a video together with a human and a conspecific subsequently approach that individual faster or spend more time in their proximity than when they had attended to something different.	<i>Pan troglodytes</i>
Hayashi et al. (2020)	5	Macaques' implicit gaze bias anticipates others' false-belief-guided actions, which is abolished by chemogenetic silencing of the medial prefrontal cortex.	<i>Macaca fuscata</i>
Ryan et al. (2020)	3	There were significant positive relationships between time spent viewing eyes of faces in an eye tracker and number of initiations made for social interactions with peers.	<i>Macaca mulatta</i>
Brooks et al. (2020)	1	Administering oxytocin increased eye contact in bonobos but not in chimpanzees. In 5 out of 6 chimpanzees, oxytocin decreased attention to the eyes as compared to the mouth.	<i>Pan troglodytes</i> <i>Pan paniscus</i>
Kano et al. (2021; article written in Japanese)	1	Humans and chimpanzees looked at similar elements in the movies, including targets of actions, animal figures, and the center of abstract figures. Humans exhibited a strong "center bias" by maintaining their gaze in the center of the screen, while chimpanzees did so less.	<i>Pan troglodytes</i> <i>Homo sapiens</i>
Hepach et al. (May 2021)	5	Chimpanzees' pupil diameter decreased soon after they helped another individual. Unlike children, chimps' pupils remained more dilated when watching a third party provide help instead of them.	<i>Pan troglodytes</i>
Lewis et al. (2021)	2	Chimpanzees and bonobos preferentially attended to familiar versus unfamiliar conspecifics when viewing the sex that typically occupies the highest dominance rankings: males for chimpanzees, and females for bonobos. They did not demonstrate biases in attention between familiar and unfamiliar members of the subordinate sex.	<i>Pan troglodytes</i> <i>Pan paniscus</i>
Sato et al. (July 24, 2021)	3	Although apes did not differentiate their gaze patterns between possible and impossible elbow movements, some apes did look at elbows for longer when viewing impossible versus possible robot movements.	<i>Pan troglodytes</i> <i>Pan paniscus</i>
Lewis et al. (in prep, Social Memory)	2	Apes spent significantly longer looking at images of their previous groupmates as compared to images of unfamiliar strangers. These biases were not impacted by duration apart, and results indicate that recognition of previous groupmates persists for at least 26 years. Apes' attention biases were also stronger for individuals with whom they had more positive social interactions.	<i>Pan troglodytes</i> <i>Pan paniscus</i>
Lewis et al. (in prep, Names Study)	2	Bonobos and chimpanzees looked for longer durations at the image of the individual whose name was called as compared to the image of the distractor individual 2 s after the call ended.	<i>Pan troglodytes</i> <i>Pan paniscus</i>

Note: Review section in which the article's findings are summarized is noted in column 2.

expressions. The similarities and differences in the scanning patterns between humans and chimpanzees indicate both homologous and species-specific forms of facial communication in these species.

Kano et al. (2012) further compared the face-scanning patterns of humans, gorillas, and orangutans and found similar patterns of face and eye-scanning as the previous studies (Kano et al., 2012). Kano and colleagues presented still photographs of both conspecific and heterospecific faces and bodies while tracking subjects' eye movement patterns. When viewing whole-body pictures, all species spent longer durations viewing faces as compared to bodies and backgrounds. When viewing pictures of faces, each species viewed the inner features of the faces, especially the eye region, for longer

periods than they viewed the peripheral features (these patterns are similar to those found in chimpanzees, described above; Kano & Tomonaga, 2009, 2010). There were no significant differences in viewing patterns between gorillas and orangutans, yet humans displayed some unique patterns. When viewing whole-body pictures, humans viewed the faces longer than did the nonhuman apes, and when viewing face pictures, humans viewed the eye regions longer than did the nonhuman apes (and alternated their gaze between the left and right eyes more than did the nonhuman apes). Finally, all three species fixated on conspecific faces longer than on heterospecific faces when viewing whole-body pictures. Taken together, these results indicate both general face and body scanning patterns

across these three ape species, as well as more species-specific viewing patterns.

Kano and colleagues (2015) also compared the social attention patterns of chimpanzees and bonobos when viewing conspecific and heterospecific faces (Kano et al., 2015). They presented both species with 90 images of conspecific and heterospecific faces and full bodies, and found that bonobos viewed the eyes and faces longer than chimpanzees did, whereas chimpanzees viewed the action objects handled by the model apes (e.g., food, tools, toys) and anogenital areas longer than bonobos did. Even in images that contained action objects and anogenital regions, bonobos viewed faces longer, suggesting that they actively maintained their attention to the face and eye regions. Bonobos first rapidly fixated to the eyes while chimpanzees first rapidly fixated to the mouth region, and bonobos viewed the eyes longer for both conspecific and heterospecific images. Bonobos' rapid fixation to the eyes is similar to patterns seen in both children and adult humans (Farroni et al., 2002; Fletcher-Watson et al., 2008; Hershler & Hochstein, 2005), gorillas, orangutans, and rhesus macaques (Guo, 2007; Kano et al., 2012). These species-specific attentional patterns that have emerged in chimpanzees and bonobos may shape the development and evolution of both cognition and behavior in significant ways in these species. Interestingly, chimpanzees' focus on actions over faces is also evident in their attention to goal-directed actions (Myowa-Yamakoshi et al., 2012).

Similar scanning patterns have since been found in other comparative noninvasive eye-tracking studies with humans, chimpanzees, gorillas, orangutans, macaques, and titi monkeys (Kano & Tomonaga, 2011b; Kano et al., 2011, 2021; Mühlenbeck et al., 2016; Ryan et al., 2019). First, the results from these studies indicated that macaques, titi monkeys, and apes attend more to videos with social stimuli as compared to pictures with social stimuli, and that juvenile macaques and titi monkeys attend more to social stimuli as compared to other age groups. This research also replicated the effect that chimpanzees had shorter fixations on each presented image and thus were able to view a greater number of images as compared to humans, irrespective of stimulus type. Similarly, orangutans processed the presented symmetric and asymmetric stimuli faster than did humans, and scanned a larger area of the screen compared to humans.

Comparable findings were demonstrated with an experiment using the gap-overlap paradigm, which is used to examine the competition that arises between choosing to fixate on a single point or choosing to shift gaze from this point to another one. In this study, chimpanzees, gorillas, orangutans, and humans were presented with the same type of stimulus at the center and periphery of the screen (Kano et al., 2011). In the gap condition, there was a delay between the presentation of the central stimulus and the peripheral stimulus; in the overlap condition the central and peripheral stimuli were presented concurrently. Here, the delay in shifting gaze from the central stimuli to the peripheral stimuli was significantly longer during the overlap condition than under the gap condition for humans, and this "gap effect" was significantly greater for humans as compared to

the other apes across stimulus types (Kano et al., 2011). This suggests that many nonhuman great ape species have similar motor and perceptual abilities for responding to stimuli that are presented peripherally. These patterns were not dependent on stimulus type, indicating these perceptual and mechanistic differences during the overlap condition are generalizable across various types of visual input. The species-differences in the timing of gaze shifts when viewing naturalistic scenes and sequential stimuli may reflect divergent processing patterns between humans and other great apes.

As human and nonhuman great apes occupy distinct environments, the authors hypothesize that these species-differences in the timing of gaze shifts might be due to disparate requirements for search strategies. As great apes habitually live in dense forests where encounters with unfamiliar conspecifics and dangerous animals are unpredictable, faster scanning mechanisms may allow them to more quickly process a greater area and number of stimuli in their environment. In contrast, humans may exhibit prolonged fixations that reflect higher-level processing such as language processing and information integration (Kano et al., 2011).

Further, Kano and Tomonaga conducted a comparative eye-tracking experiment with chimpanzees and humans to understand the perceptual mechanisms underlying gaze guidance in great apes. They showed both species images that had been manipulated from their original form in an attempt to understand how scanning patterns shifted based on different manipulations (Kano & Tomonaga, 2011a). The authors presented both species with still images of humans that were either normally presented (as a control) or that had been manipulated in the following ways: monochrome, line drawing, schematic, blurred, silhouette, upside down, scrambled, and a headless human figure. As with previous experiments, both chimpanzees and humans scanned the body and faces of the human figure more than the background, and humans showed a higher proportion of fixations to the body and face than did chimpanzees. However, none of the image manipulations significantly altered the scanning patterns of chimpanzees or humans, as they continued to have a high tendency of viewing the face in all images presented (including the area where the face *should* have been in the headless image). These results suggest that both species use multiple strategies and cues to perceive the faces of individuals and have similar perceptual mechanisms to guide their gaze scanning patterns.

Howard and colleagues (2017) used noninvasive eye-tracking to examine how the presence of social agents influences memory for concurrently presented events. Gorillas and chimpanzees were first familiarized with videos of a hand (social condition) or a mechanical claw (nonsocial condition) building a block tower (Howard et al., 2017). The authors then presented the completed block tower next to a new block tower. In such paradigms, greater attention to the new tower is taken as evidence of memory for the original tower. Interestingly, apes showed this pattern only in the social condition. This same "social memory bias" result was also replicated with capuchins (*Sapajus apella*, Howard et al., 2018). Thus, the mere presence of social agents influences how primates encode information from complex scenes.

The combination of the results from these studies exploring gaze and scanning patterns in a diverse array of primate species points to both deeply evolutionarily conserved mechanisms of attention, as well as more species-specific gaze patterns. Specifically, when viewing social stimuli chimpanzees and humans generally view the informative regions, like faces and bodies, more than the background. Both species also first look at the face region before attending to other parts of the image. Humans and bonobos both devote more attention to the eye region, whereas chimpanzees attend more to the mouth when viewing images with social agents and emotional expressions. Chimpanzees also scan images more quickly and broadly than do humans. Thus, noninvasive, restraint-free eye-tracking has revealed that humans and nonhuman apes exhibit both striking similarities and important differences in attentional patterns when viewing social stimuli.

3 | DISCRIMINATION AND KNOWLEDGE OF SOCIAL AGENTS

At the foundation of human social cognition is the ability to not just attend to social agents but also to recognize, discriminate, and remember them (Cheney & Seyfarth, 1990). The capacity for individual recognition is also widespread in primates, and noninvasive eye-tracking research has further illuminated the social information that primates use to recognize and discriminate between individuals. Traditional studies on individual recognition use discrimination paradigms in which subjects experience stimuli from two different classes of conspecifics, such as playbacks of vocalizations of familiar groupmates or unfamiliar conspecifics (Godard, 1991). Biased attention or responding to one class of stimuli provides evidence that subjects can distinguish between the two. Noninvasive, restraint-free eye-tracking allows researchers to test similar questions using visual (and sometimes also auditory) information. For example, preferential-looking paradigms measure biases in attention toward one of two side-by-side images. To examine individual discrimination, most work has presented images of faces which communicate individual identity as well as aspects of health, emotion, social status, and age (Jones et al., 2012; Rhodes, 2006). Face processing in primates is cognitively complex, and while some aspects may be homologous with that of humans, recent research suggests that other mechanisms may be more divergent or species-specific (Parr, 2011).

Noninvasive eye-tracking studies have revealed that some primates can discriminate between other individuals based on several different kinds of socially relevant information. For example, Lewis and colleagues (2021) have shown that chimpanzees and bonobos can discriminate between familiar and unfamiliar individuals. They presented chimpanzees and bonobos with side-by-side images of a familiar and unfamiliar conspecific of the same sex. Both species attended more to images of their groupmates as compared to images of strangers, specifically when viewing individuals of the dominant sex (i.e., male chimpanzees and female bonobos). These findings

corroborate other evidence of individual recognition in great apes while also highlighting the socioecological pressures that shape ape social attention (Lewis et al., 2021). In another study, Kawaguchi and colleagues presented chimpanzees and bonobos with naturalistic images of both conspecific and heterospecific mother–infant pairs (Kawaguchi et al., 2019). They found that chimpanzees preferentially attend to infant over adult faces when viewing conspecific but not heterospecific images. In contrast, bonobos did not show a significant preference for viewing infant versus adult faces. Intriguingly, chimpanzee's preferential bias disappeared when facial coloration was matched between conspecific infants and mothers in the images. These findings suggest that chimpanzees can discriminate conspecifics of different age classes but that their resultant attentional biases may be shaped by attraction to species-specific infantile coloration. In a similar study, Lonsdorf and colleagues presented capuchins with a two-image preferential looking task to measure attention toward an unfamiliar male and unfamiliar female conspecific (Lonsdorf et al., 2019). Subjects showed significant biases toward members of their own sex, suggesting that capuchins can discriminate conspecifics on the basis of sex and are more attentive to potential competitors as compared to potential mates. Collectively, these studies show that some primate species attend to familiarity, age class, and also the sex of social agents.

However, other eye-tracking research suggests that apes have more detailed representations of these individuals. For example, a study by Lewis et al. (*in prep*) demonstrates that chimpanzees and bonobos have robust long-term memory for familiar individuals. In a preferential looking paradigm, apes looked significantly longer at the faces of former groupmates (who no longer lived at their institution) as compared to faces of sex-matched strangers, indicative of recognition (Lewis, Wessling, et al., *in prep*). Surprisingly, the duration since the subject had last seen the former groupmate did not influence the looking bias, suggesting consistent recognition across the range of times apart that could be opportunistically included in the design. Although the majority of trials presented groupmates from whom the participants had been separated for up to a decade, evidence of recognition was consistent even in a pair who had not seen each other for over 26 years. The authors also found that apes' looking biases were stronger toward previous groupmates with whom they previously had higher levels of positive social interaction. These findings provide evidence that chimpanzees and bonobos have enduring representations of familiar conspecifics that capture information about relationship quality specific to individual dyadic relationships.

Research also suggests that these representations integrate information across sensory modalities. After hearing the vocalization of a familiar conspecific or human, macaques preferentially attended to an image of the vocalizer over another individual (Sliwa et al., 2011). This cross-modal matching, also found in other paradigms in chimpanzees and other species (Hashiya, 1999; Kojima et al., 2003), suggests that primates have unified representations of familiar individuals that capture both auditory and visual signatures of identity. With these insights in mind, Lewis and colleagues asked

whether chimpanzees and bonobos track not only familiar conspecifics' vocalizations but also *third-party* communication that refers to those familiar individuals (Lewis et al., in prep). Apes heard a caretaker calling a familiar conspecific's name and could attend to an image of that conspecific's face or the face of another groupmate. While the mixed results did not license any firm conclusions, studies of this kind highlight the novel avenues of research that are enabled by eye-tracking.

Based on the eye-tracking research reviewed above, monkeys and great apes seem to have capacities for recognizing, remembering, and discriminating between social agents. Critically, although some previous work had probed individual recognition and memory using nontechnical paradigms, noninvasive eye-tracking has permitted substantial advances in our knowledge of these capacities.

4 | FOLLOWING SOCIAL CUES

Having established that many primates represent and remember familiar social agents, we now turn to the ways in which they respond to and process information from those social agents. Sensitivity to the social cues produced by others is an important underlying ability for higher cognitive capacities, such as theory of mind and communication. Social cues, such as gestures, transfer information related to the signaler's intent. By tracking others' gaze (or gaze-following), one can identify predators, competitors, food, or mating opportunities—and can also infer the gazer's desires and knowledge (Bettle & Rosati, 2019; Bräuer et al., 2005; Burkart & Heschl, 2006; Emery et al., 1997; Kano & Call, 2014a; MacLean & Hare, 2012; Okamoto-Barth et al., 2007; Tomasello et al., 1998, 2001). Humans begin to reflexively follow the gaze of others starting at 6-months-old; the early emergence of this behavior suggests that it may be evolutionary conserved and thus likely present in other primate species as well (Baron-Cohen, 1997; Butterworth & Jarrett, 1991). Previous studies using behavioral methods have demonstrated that gaze-following is present across many nonhuman primate species, including monkeys and apes (Anderson & Mitchell, 1999; Bettle & Rosati, 2019; Deaner & Platt, 2003; Emery et al., 1997; Ferrari et al., 2000; Tomasello et al., 1998; but see Tomonaga, 2007; Tomonaga & Imura, 2009).

However, eye-tracking has permitted precise examination of this phenomenon. Machado et al. (2011) conducted an examination of attention to social cues in rhesus macaques using light-restraint eye-tracking methods (with a noninvasive primate chair and head restraint). They found that videos with subject-directed social cues (i.e., aggressive or submissive facial expressions) captured more attention than videos depicting other social scenes, and generated larger pupil diameters which indicates heightened physiological arousal.

In the first restraint-free eye-tracking study to explore gaze-following in nonhuman primates, Hattori et al. (2010) tested whether model identity shaped gaze-following of humans and chimpanzees (Hattori et al., 2010). They presented chimpanzees and humans with

images of familiar conspecific and heterospecific models in a crouched position with an unidentifiable object on either side of the model. The images included models in one of three different postures: neutral looking straight ahead, looking toward one of the two objects (the “target” object), and reaching toward one of the two objects. They found that the identity of the model modulated the chimpanzees' gaze-following behaviors, such that they looked at the target object significantly longer than the distractor object when the model was a chimpanzee as compared to when the model was a human. However, humans were equally sensitive to the gaze cues of both models, and both species followed reaching gestures, whether the model was a conspecific or heterospecific.

A related eye-tracking study compared gaze-following of conspecific and allospecific models in humans (12-month-olds and adults), bonobos, chimpanzees, and orangutans (Kano & Call, 2014a). While tracking their gaze, the experimenters presented study participants with a video of a model turning its head repeatedly to one of two objects on either side of the screen. They first found that all ape species followed the gaze of conspecific models, but the chimpanzees did not follow the gaze of humans (while bonobos did). In line with the previous demonstration that bonobos make more eye-contact than chimpanzees (Kano et al., 2015) and previous demonstrations of species differences in gaze following (Herrmann et al., 2010), overall, bonobos responded more reliably to both conspecific and human gaze as compared to chimpanzees. In other experiments, bonobos, orangutans, and human adults followed the gaze of the other nonhuman ape species but chimpanzees (and human infants) again did not. Critically, the preferential gaze-following of conspecific models in chimpanzees and human infants was modulated by their prolonged viewing of the faces of conspecific models. This suggests that both chimpanzees and human infants have a motivation to preferentially attend to conspecific faces, which in turn shapes their patterns of sensitivity to the social cues of others.

Finally, in a more recent study experimenters used noninvasive eye-tracking to determine whether human ostensive signals enhanced gaze-following in chimpanzees, bonobos, and orangutans (Kano et al., 2018). Ostensive signals are cues made by a communicator to signal to an addressee that they intend to communicate with them; they are important for establishing a successful communicative interaction by alerting an addressee to dedicate attention to the communicative interaction. Some have argued that ostensive communication is fundamental to a human adaptation for natural pedagogy (Csibra & Gergely, 2009). Ape participants were presented with videos in which a human actor made either an ostensive cue (by making eye contact or calling the participant's name) or was presented with a control attention-getter. Then, the actor looked at one of two objects presented on either side of the screen (the “target” object). Overall, chimpanzees followed the actor's gaze to the target object, but the human's ostensive signals did not enhance gaze-following to the target object. However, following the ostensive cue, chimpanzees spent more time attending to both the target object and the distractor object as compared to the control condition—despite similar attention in preceding phases of

both conditions. These findings suggest that chimpanzees may expect the ostensive signals to precede information about the objects, triggering greater attention to both objects in this condition. However, their expectations appear to be more limited than those already observed in human infants, who show heightened attention to the specific intended referent of the actor's gaze following ostensive cues (Topál et al., 2009). Overall, noninvasive eye-tracking has provided multiple fruitful approaches for deepening understanding on nonhuman primates' attention and responses to others' social cues, such as gaze, gesture, and ostensive signals.

5 | TRACKING PERSPECTIVES AND PREDICTING BEHAVIOR

These social cues provide a window into an agent's mind. By tracking another agent's attention, it is possible to infer what they are thinking. Humans identify what an agent has or has not seen—and accordingly what she is knowledgeable or ignorant about—based on the agent's visual orientation (Carpenter et al., 1998; Tomasello, 1995). This ability to infer the internal mental states, such as desires and beliefs, that motivate others' actions is known as theory of mind or mindreading (Premack & Woodruff, 1978). Theory of mind allows us to interpret, predict, and even manipulate others' behavior across competitive and cooperative contexts (Schmelz & Call, 2016). It is also central to many of the social traits that appear to be unique to humans, such as language, teaching, cumulative culture, and cooperation involving shared intentionality (Krupenye & Call, 2019). As a result, researchers have long been interested in determining the extent to which theory of mind is also unique to our species and might explain the presence of other unique social phenomena.

Although the precise mechanisms continue to be debated (Andrews, 2016; Call & Tomasello, 2008; Heyes, 2015; Krupenye & Call, 2019; Martin & Santos, 2016; Penn & Povinelli, 2007), diverse behavioral tasks have provided evidence that great apes and some monkeys are sensitive, in some sense, to others' goals, perception, and knowledge (Lewis & Krupenye, in press). However, until recently there was no evidence that primates could track others' beliefs (Call & Tomasello, 2008; Martcorena et al., 2011; Martin & Santos, 2016). Belief representation is of particular interest because beliefs can be false (e.g., when Jean falsely believes that there are cookies in the cabinet, because she did not witness her brother eating all of them). Tracking others' beliefs therefore requires an appreciation that others can be guided by representations of the world that are independent of one's own and distinct from reality. In classic tasks designed to measure false belief understanding in human children, such as the Sally-Anne task (Baron-Cohen et al., 1985), participants witness events like the following: Sally hides her marble in a basket and then goes out to play and, while she's away, Anne moves the marble from the basket to the box. Human mindreaders viewing these events can simultaneously represent (1) that Sally believes her marble to be in the basket, where she left it,

and (2) that her marble is actually in the box, where Anne subsequently moved it during Sally's absence. In humans, an understanding of false beliefs is typically assessed by asking participants to verbally predict the behavior of an agent who has one (e.g., 'When Sally returns to retrieve her marble, where will she look for it?') (Baron-Cohen et al., 1985). For example, a mindreader capable of representing others' beliefs should know that Sally will search for her marble in the basket, where she believes it to be, even though the mindreader is aware that it is no longer there. Comparative cognition researchers have crafted ingenious paradigms in their efforts to assess whether primates, too, can predict the behavior of an agent with a false belief (e.g., Hare et al., 2001; Kaminski et al., 2008). However, even the most elegant of behavioral paradigms necessarily places high memory and inhibitory control demands on subjects, which may have contributed to their failure in false belief tasks (Kano et al., 2017, 2020).

Excitingly, noninvasive eye-tracking has delivered tools for nonverbally measuring participants' predictions under minimal cognitive and motor demands. Humans and other animals naturally look to locations where they expect events to imminently happen, even before those events occur. For example, chimpanzees and bonobos watching a movie for a second time remembered and anticipated the course of events: they looked to specific locations where a dynamic event was about to occur before it actually happened (Kano & Hirata, 2015). This phenomenon, known as anticipatory looking, has also demonstrated that apes anticipate the goal-directed actions of other social agents (Kano & Call, 2014b; Myowa-Yamakoshi et al., 2012). After viewing a hand or mechanical claw repeatedly grasp one object over another, when the object locations were switched, apes expected the hand but not the claw to continue to seek the same goal object (Cannon & Woodward, 2012; Kano & Call, 2014b).

The versatility of anticipatory looking has made it an exciting paradigm for testing participants' predictions, even about agents with false beliefs (e.g., Surian & Geraci, 2012). Importantly, stimuli can be carefully controlled to alleviate demands on memory and inhibitory control and the use of gaze alone further minimizes inhibitory control and motor demands. To test chimpanzees', bonobos', and orangutans' capacity to predict the behavior of an agent with a false belief, Krupenye and colleagues developed an anticipatory looking test (Krupenye et al., 2016). Given apes' intrinsic interest in social information, false belief manipulations were embedded within engaging movie stories involving conflicts between a human protagonist and an antagonist in a gorilla costume. For example, after a brief fight, the gorilla stole the human's stone and hid it in one of two boxes. While the human was subsequently away, the gorilla moved and ultimately removed the stone. Across several conditions and studies, when the human returned to search for his stone (or other goal object) and ambiguously approached the two possible hiding locations, apes looked to the location where the human believed the object to be, in anticipation of his search. This was true even though apes closely visually tracked all events and never saw the human actually search

in either location. This finding has been replicated in one species of monkey, the Japanese macaque (Hayashi et al., 2020). Subsequent work has sought to clarify whether the predictions demonstrated in these first studies reflect the same kinds of belief representation mechanisms that exist in humans. For example, one follow-up study provides evidence that these mechanisms are not just domain-general cueing effects (i.e., spontaneous responses, triggered by perceptual features of the stimuli) but specifically track social information (Heyes, 2017). When shown nonsocial versions of the aforementioned false belief manipulation, apes did not show the same targeted patterns of anticipatory looking (Krupenye et al., 2017). Another study provided some evidence that apes may have been tracking others' mental states rather than their behavior. Apes seemed to interpret whether a human agent could see through a new barrier, specifically depending on whether apes had previously experienced that barrier to be opaque or see-through (Kano et al., 2019). After watching the same exact video, apes showed different patterns of anticipatory looking depending on their personal experience with the barrier in the video.

Across humans and other animals, anticipatory looking has generated substantial knowledge of social and physical cognition. Although the majority of paradigms and uses of anticipatory looking (e.g., to measure predictions of others' goal-directed actions) have proven robust and replicable, there have been some failures to replicate anticipatory looking tasks designed to measure false belief understanding, especially in human infants (Baillargeon et al., 2018; Kulke & Rakoczy, 2018). This ambiguity has inspired a large-scale ManyBabies effort to confirm the replicability of these effects in human children (Kulke & Rakoczy, 2018). While some have wondered whether replicability issues could extend to paradigms in other animals (Horschler et al., 2020), to date these effects have proven replicable, perhaps because comparative studies have reliably used more engaging, socially dynamic stimuli (Kano et al., 2020). Moreover, while a "file-drawer" problem, in which negative findings are not always published, has hindered inferences about the reliability of specific findings in humans, as far as we know, the comparative literature on anticipatory looking false belief tests is comprehensive, elevating confidence in published effects. That being said, as this important tool continues to be adapted to address an ever-growing number of exciting questions about primates' predictions (e.g., Cheney & Seyfarth, 1980; Thomas et al., 2022) and the cognitive representations that underlie them, researchers should carefully attend to factors that may elevate robustness and replicability of findings (see also: Farrar et al., 2021).

While we have much to learn about the nature and limits of nonhuman mindreading, taken together, this research shows the powerful contribution that eye-tracking has made to our understanding of social prediction and cognition in nonhuman primates. By lowering the task demands that arise from behavioral methods, noninvasive eye-tracking research allows for new, useful ways to explore some of the most complex forms of social cognition in nonhuman primates.

6 | NEW APPROACHES TO THE COMBINATION OF NONINVASIVE EYE-TRACKING AND OTHER PHYSIOLOGICAL OR BEHAVIORAL METHODS TO EXPLORE PRIMATE SOCIAL ATTENTION

A particularly exciting use of noninvasive eye-tracking is in combination with other metrics and techniques, allowing for a deeper understanding of complex phenomena. Researchers have utilized innovative combinations of noninvasive eye-tracking methods and other physiological and behavioral measures to further investigate patterns of attention in primates. For example, Brooks and colleagues conducted a study in which they presented chimpanzees and bonobos with conspecific images and videos while tracking their gaze (Brooks et al., 2021). In addition, they administered intranasal nebulized oxytocin (or saline in the control condition) directly before presenting the conspecific images and videos. The authors found that the intranasal administration of oxytocin increased attention to the eyes in bonobos but not in chimpanzees. Intriguingly, all but one chimpanzee participant decreased looking duration to the eyes relative to looking duration toward the mouth. In this way, it seems that oxytocin operates differently in these two species and seems to enhance species-typical viewing patterns of faces.

To examine evolutionary foundations of a concern for others, Sato and colleagues (2019) presented chimpanzees with images of injured and noninjured conspecifics, along with real-life demonstrations of a familiar human experimenter injuring themselves (including scenes with fake blood/open wounds and without these explicit cues). First, Sato and colleagues found that chimpanzees attended more to images of injured conspecifics as compared to images of noninjured conspecifics, but this pattern disappeared when the images of the injury were scrambled but the color information was maintained. This study also utilized thermal imaging to detect chimpanzees' physiological responses to others' injury. When viewing the realistic live demonstration of a familiar human experimenter experiencing an injury, chimpanzees' nasal temperature decreased significantly more than in a control condition without injury. However, this pattern disappeared when there were not explicit cues of injury such as blood or an open wound. A decrease in nasal temperature indicates arousal due to an activation of the sympathetic nervous system (Ioannou et al., 2015). Thus, these findings indicate that chimpanzees attend more to injured conspecifics than noninjured conspecifics, and that they are physiologically aroused by a familiar human's injury with explicit injury cues. Taken together, these results suggest that chimpanzees investigate others' injuries in familiar situations (i.e., with explicit cues of injury) not only out of interest but possibly also out of empathy. These findings are similar to those in humans, which imply that images of injury may be associated with feelings of empathetic pain rather than disgust (Kupfer, 2018).

Two further studies used physiological measurements recorded with eye-tracking—changes in pupil size—to examine chimpanzees' response to and engagement with other agents. Kret et al. (2014)

presented humans and chimpanzees with short video clips of the eyes of conspecifics and individuals of the opposite species (Kret et al., 2014). The pupils of the agent presented in the videos either slightly dilated or constricted, and the authors found that subjects' pupils adjusted to match those of the videos. That is, both humans and chimpanzees mimicked the pupil-size of the pupil in the video, especially when viewing clips of their own species. This effect was strongest for humans and chimpanzee mothers, and suggests that pupil mimicry—a propensity involved in synchrony and coordination—is deeply conserved in the great ape lineage but has likely gained even more importance for successful social interactions in humans.

In a more recent study, Hepach and colleagues (2021) used pupil dilation as a measure of physiological arousal. The authors sought to determine whether chimpanzee helping behaviors, observed in experimental and observational contexts, might be underlain by an intrinsic internal motivation, as they are in humans (Hepach et al., 2021). Here, they provided chimpanzees with an opportunity to help a conspecific obtain food, and measured chimpanzees' pupil diameter at multiple points throughout the process. They found that chimpanzees' pupil diameter decreased soon after they had helped a conspecific. However, their pupils remained dilated after watching a third party help their conspecific, unlike humans, whose pupils decrease in diameter after watching a third party help. The authors conclude that this pupil dilation pattern indicates that chimpanzees' helping may be motivated by direct or indirect reciprocity, as their internal arousal (as measured by pupil dilation) remains elevated when they themselves cannot help a conspecific.

Research has also shown that gaze metrics are predictive of subsequent social behavior, both on immediate and longer time-scales. For example, Ryan et al. (2020) found that in infant male rhesus macaques, there was a significant positive relationship between the time spent attending to faces (as measured with an eye-tracker) and the number of initiations made for social interactions with peers between 3 and 6 months of age (Ryan et al., 2020). These results indicate that noninvasive eye-tracking can be a useful tool in linking patterns of attention to individual differences in social behavior across longer time-scales. Attention has also been shown to influence immediate social preferences on shorter time-scales. Wolf and Tomasello (2019) found that chimpanzees who watched a video together with a human or conspecific subsequently approached more quickly or spent more time in proximity to the partner than when they had not previously shared attention to the same stimulus (Wolf & Tomasello, 2019). Taken together, these findings reveal the behavioral outcomes of various patterns of attention in primates' complex social environments, on both immediate and longer time-scales.

In addition, there are still numerous and exciting combinations of noninvasive eye-tracking and other behavioral and physiological methods to be explored. For example, with the right materials eye-tracking can be combined with other measures of arousal such as thermal imaging (e.g., de Vevey et al., 2022) to synchronously investigate eye-gaze patterns and physiological arousal. Eye-tracking can also be conducted alongside other physiological measures like breathing rate, heart rate, or salivary cortisol and oxytocin levels (e.g.,

Aureli et al., 1999; Preis et al., 2018) to provide more comprehensive insights into primates' responses to cognitive tasks. Behavioral measures such as self-scratching and yawning (e.g., Yamanashi & Matsuzawa, 2010) can also be recorded alongside eye-tracking measures to integrate gaze patterns and behavioral responses. Pairing eye-tracking data with behavioral measures could allow for a deeper understanding of how gaze patterns and behavior may affect one another, which is not possible with only one kind of data alone. Finally, combining eye-tracking methods with touchscreen tasks would allow us to understand how attention and visual information-gathering inform the decisions that animals make in cognitive tasks.

As we have highlighted throughout this paper, noninvasive eye-tracking offers a powerful and precise technique for investigating attention and social cognition under highly standardized conditions. By combining noninvasive eye-tracking with other metrics and techniques, researchers have been able to triangulate findings and deepen understanding of complex multicomponential phenomena. This research, just in its infancy, has begun to clarify the physiological underpinnings of behavior and relationships between attention, cognition, and behavior. The combination of noninvasive eye-tracking and behavioral or other physiological measures has allowed for the exploration of numerous similarities and differences in the ways in which primates of different species attend to and process social events. Ultimately, this research shows that, like humans, primates show strong interest in social features of stimuli and their social attention influences both their subsequent behavior and memory.

7 | SUMMARY AND FUTURE DIRECTIONS

Tremendous gains in our knowledge of primate social cognition have already been made with the use of noninvasive eye-tracking methodology techniques. These efforts have led to a deeper understanding of the similarities and differences in gaze patterns between humans and other nonhuman primates. Critically, humans tend to fixate for longer on socially relevant stimuli and regions, often in the center, while great apes exhibit shorter fixation durations, more fixations per second, and a broader distribution of fixations across a stimulus. In addition, many primate species tested so far, while demonstrating some species-specific tendencies, generally tend to focus on a social stimulus compared to the background of an image, the face as compared to the body of a social agent, and the socially relevant features of the face, including the eyes and mouth. These foundational findings supported further exploration of how nonhuman primates discriminate between and build knowledge of social agents. This research demonstrates that nonhuman primates can discriminate between familiar and unfamiliar individuals, male and female conspecifics, and conspecific mothers and infants. Scientists have also explored the extent of great ape long-term social memory, which can last for at least a decade and is shaped by social relationships. Findings from noninvasive eye-tracking studies

have uncovered primates' ability to recognize conspecifics using multiple modalities, and their possession of multimodal representations of identity that integrate visual and auditory information. Building on findings from nontechnical methodologies, more recent eye-tracking research has shown that many nonhuman primates can follow gaze, even that of nonconspecifics, and can respond appropriately to other social cues. In some species, following social cues is biased toward conspecific cues, just as it is in human infants. Finally, the most recent noninvasive eye-tracking research has determined that great apes and at least one monkey species can track information relevant to others' perspectives to predict their behavior, making anticipatory looks that indicate that they may understand that others can hold false beliefs.

Although many species have already been included in studies exploring and comparing gaze patterns, testing a wider array of species on their basic visual and gaze mechanisms would help to further elucidate the evolutionary trajectory of these patterns and the selective pressures that have helped to shape them. A majority of the restraint-free noninvasive eye-tracking research has thus far been conducted with apes and, to a lesser extent, rhesus macaques. Given the applicability of noninvasive approaches across species and research contexts (e.g., including zoos and sanctuaries), future research should incorporate a larger variety of primate species, including gibbons, monkeys of the Americas, monkeys of Afro-Eurasia, and lemur species. Clarifying the phylogenetic distribution of social cognition is fundamental not only for understanding individual species but also for reconstructing the evolutionary history of these traits and identifying the socioecological pressures that vary with them.

The foundations of noninvasive eye-tracking research with primates reviewed here lay the groundwork for new questions, hypotheses, procedures, and tests with additional species. For example, eye-tracking research with chimpanzees and bonobos has already begun to explore their knowledge of the communication, dynamics, and relationships among their groupmates (Lewis et al., in prep). This study explores whether chimpanzees and bonobos can recognize the keeper-given names of their groupmates, as evidenced by preferential looking toward an image of a groupmate whose name was called. Countless human paradigms are also waiting to be adapted for nonhuman primates, and new, original paradigms waiting to be invented. Eye-tracking can also provide other nonverbal measures of participants' predictions, such as their attention and arousal in response to expected and unexpected events (Krüger et al., 2020; Marticorena et al., 2011). Research that combines physiological measurements such as pupillometry or thermal imaging with gaze-tracking or combines gaze-tracking with other tools like touchscreens can help further elucidate the connection between motivation, attention, and cognition. Lastly, as the wealth of primate eye-tracking data builds, in the future we may be able to start utilizing these data and methods to provide more insight into the cognitive and physical health of primates. Just as in humans, an understanding of healthy and neurotypical gaze and attention patterns could help to identify patterns that are less

typical and perhaps stem from neuro-divergence in primates (Boraston & Blakemore, 2007). As we have shown here, restraint-free, noninvasive eye-tracking is a powerful tool helping to answer a diverse host of questions, old and new, by supplying often highly simplified experimental paradigms for capturing elusive phenomena. And, critically, its untapped potential is even greater than the body of discoveries that it has already delivered. Indeed, eye-tracking will allow for decades of exciting insights into the minds and behavior of humans and our closest primate relatives.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

PEER REVIEW

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