

# Looking past the model species: diversity in gaze-following skills across primates

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Primates must navigate complex social landscapes in their daily lives: gathering information from and about others, competing with others for food and mates, and cooperating to obtain rewards as well. Gaze-following often provides important clues as to what others see, know, or will do; using information about social attention is thus crucial for primates to be competent social actors. However, the cognitive bases of the gaze-following behaviors that primates exhibit appear to vary widely across species. The ultimate challenge of such analyses will therefore be to understand *why* such different cognitive mechanisms have evolved across species.

## Addresses

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Fundamental to the study of comparative cognition is the idea that many species may exhibit behaviors that appear similar, even if the psychology underlying those behaviors differs across taxa. This distinction is testament to the ingenuity of evolution: the hard problems that animals face get solved, even if the solution is not always the same and some species consequently possess more flexible cognitive mechanisms than others. It also highlights the importance of thinking about primate social interactions not only in the context of behavioral evolution – the special things that primates do – but also in terms of cognitive evolution—the special ways that primates think. We use this framework to analyze the gaze-following behaviors that primates exhibit in naturalistic contexts, the cues they use when co-orienting with others, and the cognitive skills that underlie gaze-following and feed into their social decision making. Research already suggests there is no ‘model primate,’ as current evidence indicates that different species – including those that are closely

related to each other – likely use different types of gaze information and show different levels of understanding when using such information across contexts.

## Gaze-following skills are widespread

Gaze-following – or looking in the direction that others are looking – can result from mechanisms ranging from involuntary capture of attention when others shift where they are looking, to shared attention in which two or more observers know they are jointly looking at the same object or event [1\*\*]. Whether it involves low level processes or more sophisticated social-cognitive skills, gaze-following allows individuals to apprehend things like food sources, predators, and conspecifics that others have detected in the environment, and thus lets individuals to exploit information that others have acquired about the world to which they might not otherwise have access. Across human and nonhuman primates, this phenomenon has been assessed in a variety of ways, both observationally – examining co-orienting behaviors between conspecifics in natural social groups – and experimentally—from the use of simple photographs in which social partners are looking one way or the other, to more complex paradigms that examine whether individuals can follow gaze around barriers and adjust their own position to determine what others are looking at [2].

Converging evidence from these different paradigms indicates that many primates are at least behaviorally responsive to the direction of others’ gaze as indicated either by the orientation of their eyes, head, or body. At the most basic level, at least some species from each major primate radiation spontaneously follow the gaze of human experimenters or conspecifics. Hominoids including humans, chimpanzees (*Pan troglodytes*: [1\*\*,3\*]), and the other great apes (bonobos: *Pan paniscus*; gorillas: *Gorilla gorilla*; orangutans: *Pongo pygmaeus*: [4\*,\*\*5]), Old World monkeys including several species of macaques (Rhesus: *Macaca mulatta*; stumptail: *M. arctoides*; pigtail: *M. memstrina* [1\*\*,6]), and mangabeys (*Cercocebus atys torquatus* [1\*\*]); New World monkeys including cotton-top tamarins (*Saguinus oedipus*: [7]) and common marmosets (*Callithrix jacchus* [8]), and even some lemur species (ring tailed: *Lemur catta* [9\*]; brown: *Eulemur fulvus* [10]; black: *Eulemur macaco* [10]; but see [11]), all follow gaze, at least in some contexts.

This suggests that a basic ability to learn about one’s environment from the gaze direction of others is common throughout the primate order. This is especially true among anthropoids (apes and monkeys), the most well

Table 1

**Gaze-following methodologies. Studies of gaze-following across primate species broken down by demonstrator species (human or conspecifics) and type (live demonstrator or photo). Studies that involve both human and conspecifics demonstrators are starred (\*).**

	Great apes	Lesser apes	Old World monkeys	New World monkeys	Strepsirrhines
Human demonstrator	Chimpanzees: [3*,4*,5**,13,14**,19–21,51,52] Bonobos: [4*,5**,14**] Gorillas: [4*,5**,14**] Orangutans: [4*,5**,13,14**]		Longtail macaques: [35*] Pigtail macaques: [37,78] Rhesus macaques: [20,37] Stumptail macaques: [11,37] Tonkean macaques: [37]	Brown capuchins: [37] White-faced capuchins: [37] Squirrel monkey: [37] Cotton-top tamarins: [7] Common marmosets: [8]	Black lemurs: [11,37] Brown lemurs: [37]
Human photo	Chimpanzees: [54]	Pileated gibbons: [53] <sup>†</sup>			
Conspecific demonstrator	Chimpanzees: [1**]		Rhesus macaques: [1**] Pigtail macaques: [1**] Stumptail macaques: [1**] Sooty mangabeys: [1**]	Cotton-top tamarins: [7] <sup>†</sup>	Ringtailed lemurs: [9*]
Conspecific photo		Pileated gibbons: [53] <sup>†</sup>	Rhesus macaques: [6,55] Diana's monkeys: [56]		Black lemurs: [10] Brown lemurs: [10]

studied group. However, an important caveat must temper this conclusion: the methodologies used to assess gaze-following often differ substantially across studies. For example, most studies use humans as demonstrators rather than conspecifics for pragmatic reasons (see Table 1), and it is possible that some species will respond differently to conspecifics and humans in social-cognitive tasks (however, note that chimpanzees appear to gaze-follow at similar rates across studies that used either a conspecific or human demonstrator; [1\*\*,12,13]). At the same time, while it is reasonable to assume that animals will show their most sophisticated cognitive skills when interacting with conspecifics, in some cases the use of human demonstrators may actually lead to *improved* gaze-following performance. For example, when co-orienting in response to eye movements, the increased visibility of human eyes (e.g. our white sclera are more salient than those of other species) may lead to an enhanced response that does not reflect what animals do in their normal social environments (see below for a discussion of the role of species differences in eye morphology).

### Different species use different gaze cues when co-orienting

Although a variety of species co-orient in response to the gaze of others, there appears to be variation in the type of gaze information that different species use to co-orient. For example, some species appear to follow shifts in eye position alone (e.g. apes [14\*\*]); however, for other species there is only solid evidence that they co-orient in response to shifts in the position of the head or even entire body (e.g. macaques [1\*\*,6]; capuchins [15]; cotton-top tamarins [7]; ring-tailed lemurs [9\*]; black lemurs [10]; brown lemurs [10]; but see [78]). This variation may stem from variability in the information that the eyes carry, partly due to differences in morphology across taxa.

Specifically, the coloration of some primate species results in low contrast between the eyes and face, whereas other species have more visible eyes; this difference might drive reliance on shifts in eye direction as a cue for social attention. Note that human eyes are especially visible owing to our large white sclera, a feature that appears to be exceptional among primates [16\*\*,17].

To test how eye morphology affects the type of cues that different species use to co-orient, Tomasello *et al.* [14\*\*] pitted different types of cues against each other and examined the gaze-following responses of nonhuman great apes and human infants. Owing to unique eye morphology, humans were predicted to be more reliant on eye gaze than other species of apes. Bonobos, chimpanzees, gorillas, and human children witnessed a human experimenter 'looking' at the ceiling with either eyes alone, face alone (with eyes closed), with both face and eyes, with face oriented up but back turned to the subject (i.e. face and eyes not visible). All conditions increased the gaze-following of all four species relative to the control (i.e. the experimenter did not look up); however, nonhuman apes were more dependent on face orientation than eye orientation, whereas children responded strongest to eye direction alone. Thus, while African apes can use eye direction alone as a cue, they are more influenced by face direction than are human children. Studies like this can thus help to differentiate the cues that various species are *capable* of using versus the cues they prefer to use when available.

Unfortunately, few studies have directly compared the response of subjects within or between species to these different types of gaze cues (i.e. eye, face, head, or body cues) in a systematic fashion. Consequently, in most cases we are only able to make qualitative judgments about

species' performance across different studies not designed for such comparisons. However, differences in eye and face morphology and species-typical socioecology (e.g., degree of arboreality) predict that species will show significant differences in the degree to which they use various types of gaze information.

### Cognitive mechanisms underlying primate gaze-following

Although gaze-following is widespread in primates, diversity in the types of gaze information that different species utilize suggest that the psychology underlying this behavior differs radically across primates. For example, humans develop the ability to flexibly model the visual perspective and attentional state of others on the basis of multiple types of social information including gaze direction [18]. This process involves reasoning about unseen entities – psychological states – that causally influence the behaviors of others. It is unclear, however, whether most nonhuman primates also use gaze information as a window into other's minds. Although there is now strong evidence that nonhuman apes understand a great deal about the visual perception of others, for the vast majority of other primate species we know very little about the potential cognitive mechanisms underlying social attention (see Table 2). In many cases, it is highly plausible that gaze-following is a fundamentally egocentric process in which animals exploit the behavioral cues provided by others in a largely reflexive manner (e.g. involuntary capture of attention; [1\*\*]).

The nature of gaze-following in chimpanzees and other nonhuman apes suggests that individuals of these species follow gaze because they understand something about the nature of 'seeing.' Apes not only direct their own gaze in the direction of others but also match their own line of sight to others when physical barriers and distracting objects obscure the target of another's gaze, sometimes requiring them to physically reorient their own bodies [3\*,19]. They may also 'check back' with the actor in an

attempt to verify the direction of the other's gaze, or quickly stop following the gaze cues when they cannot locate the target of the other's gaze [4\*,20,21]. Additionally, there is extensive evidence that apes modulate their gestures according to other's attention, adjusting gesture frequency on the basis of whether others can see them [22–24], moving in front of people in order to execute gestures in their line of sight [25], and making noises to attract the attention of conspecifics before gesturing in natural contexts [26–30]. Perhaps the strongest evidence that apes have a complex understanding of visual attention, however, comes from studies where subjects must compete with others to obtain food rewards. Chimpanzees use the visual access of conspecifics to determine which specific food to target [31\*\*], and also appear to understand how visual perceptions lead to knowledge in others [32]. When competing with humans, chimpanzees prefer to retrieve a piece of food that the human cannot see over one they can see, and even engage in attempts to disguise their interest in the food as they approach it [33,34].

In contrast with apes, many monkey species may follow the gaze of others without possessing the same rich cognitive understanding of their visual perceptions. Gaze-following in these species may result from processes that are largely egocentric or reflexive, with gaze cues capturing attention but not engaging more sophisticated social-cognitive reasoning. However, to date few species have been studied, making it difficult to draw strong conclusions. As always, the majority of work has been conducted with the ubiquitous rhesus macaque, but it is crucial to realize that there is no *a priori* reason to believe they are in any way representative of non-ape primates given the phylogenetic and socioecological diversity within the primate order (e.g. rhesus have among the least egalitarian social system of any primate). However, research with rhesus macaques has revealed that, like apes, adults quickly habituate to repeated gaze cues when they repeatedly cannot locate the target of another's gaze

**Table 2**

**The cognitive bases of gaze-following. Studies addressing gaze-following and related social-cognitive skills across major taxonomic divisions. Note that in some cases studies find negative results (e.g. [44\*] and [43] fail to find evidence that some monkeys can take the visual perspective of conspecifics).**

	Great apes	Lesser apes	Old World monkeys	New World monkeys	Strepsirrhine
Follow head/body orientation cues	[1**,3*,4*,5**,13,14**,20,21,51]	[53]	[1**,6,11,20,35*,37,55,56,78]	[7,8,37]	[9*,10,11,37]
Follow eye orientation cues	[3*,13,14**]		[78]		
Follow gaze behind barriers	[3*,4*,5**,19,58]				
Habituate to repeated looks; check back with demonstrator	[4*,5**,20,21]		[20,35*]		
Use of attentional cues (object choice and expectancy violation)	[13,21,58–63]	[53]	[38,40,57]	[7,8,15,41,42,79]	[10]
Modification of gestures to account for attention of observer	[13,22–29,52,64–69]	[70]			
Visual perspective taking	[31**,32–34,71–75]		[36*,40,76,77]	[43,44*]	

[20,35<sup>•</sup>], and they may even check back to the demonstrator if they do not at first see the target of her gaze [35<sup>•</sup>]. Moreover, competition studies similar to some of those examining chimpanzees indicate that rhesus monkeys are sensitive to the visual access of humans and avoid stealing food from a human who can see them in favor of one who cannot [36<sup>•</sup>]. However, there already is reason to suspect differences between mechanisms underlying chimpanzee and rhesus macaque gaze-following skills. A developmental comparison shows that although adults of both species follow gaze and habituate to repeated looks to an empty target, the tendency to habituate quickly develops over different time scales in the two species [20] and may involve different developmental pathways.

Meanwhile, the few studies that have been conducted with other primates suggest that their co-orienting behaviors are more egocentric and reflexive. For example, some lemur species co-orient with conspecifics during their natural interactions [9<sup>•</sup>], but seem less able to follow gaze in experimental contexts [11,37]. In addition, a number of species fail to use gaze information in violation of expectation paradigms that use looking time as a measure of discrimination (e.g. capuchins and squirrel monkeys [41]; but see positive results with cotton-top tamarins [42]), or to locate hidden food in object choice tasks [15,38–40]. Moreover, in food competition paradigms (which demonstrate that chimpanzees understand other's visual perspective) both capuchin monkeys [43] and common marmosets [44<sup>•</sup>], fail to reason about what conspecifics can or cannot see—suggesting that they egocentrically use gaze as a behavioral cue without necessarily taking the visual perspective of others.

Overall then, current evidence suggests that while chimpanzees and probably rhesus macaques know something about what others see, and use this information to guide their own behavioral decisions, other species may not have such a sophisticated understanding of attention or perception in others—even though they gaze-follow in many of the same contexts as chimpanzees and rhesus macaques. Importantly, humans may be unique among primates in their use of social information such as gaze direction in specific contexts such as those involving cooperation and communication [12,14<sup>••</sup>—suggesting that even nonhuman apes differ from humans in how flexibly they respond to the social attention of others. On the basis of results so far, we therefore predict there will be diversity in the cognitive mechanisms that underlie the gaze-following skills of primates across the order (see Table 2).

### Gazing into the future of primate research

It is an exciting time in the study of primate social cognition because we are making progress in attacking the big questions about gaze-following specifically and social cognition more generally: to what extent are social

skills shared across species (and similar or different to those found in humans), and to the extent that differences exist, *why* do different species vary in their social skills?

The first part of the question is fundamentally a phylogenetic one. While there is a growing literature on nonhuman apes and a few monkey species, little if any research has examined gaze-following skills in some groups of primates (see Tables 1 and 2), including strepsirrhines (e.g. lemurs and lorises), some groups of New World monkeys such as the atelids (e.g. howler, spider, and woolly monkeys), the colobines (e.g. leaf-eating Old World monkeys such as colobus or langurs), and the lesser apes (e.g. gibbons and siamangs). As a result, it is still difficult to characterize the phylogenetic origin of gaze-following skills with much precision beyond a few specific clades within the order. Even more valuable than gross comparisons between distantly related species will be comparisons between groups of closely related species (e.g. such as macaque species with more or less egalitarian social systems). Such research will be crucial in determining the distribution of gaze-following skills across primates – and ultimately be crucial for addressing the second part of this question – why these skills evolved.

The second part of the question is an ultimate one, and is the more challenging of the two because it requires reconstructing past events – evolutionary change and the processes that drove it – that cannot be directly observed. There are three main routes to assess the ultimate function of gaze-following skills. First, comparisons of matched pairs of closely related species that differ in a relevant evolutionary variable (e.g. social system, mating system, habitat, etc.) can assess whether such variables predict species differences in cognitive skills. For example, ecological differences such as the degree of arboreality may lead species to depend on more gross bodily cues than eye or head position, as visibility is more limited in dense foliage. Moreover, if gaze-following is important for social competency as we have claimed, then primates living in larger or more complex social groups might be expected to show superior gaze-following skills. Some evidence already suggests that this is the case: although apes all follow gaze, the use of more complex paradigms and sensitive measures of behavioral response has revealed subtle differences in performance. In a direct comparison of the ability nonhuman apes to follow gaze geometrically (around barriers and past distractions) only the African apes (chimpanzees, bonobos, and gorillas) and not the less gregarious and more distantly related orangutans behave like humans [5<sup>••</sup>].

Another important approach to addressing the ultimate question is to examine the context in which a given cognitive skill is used, as this can give clues as to its behavioral function. For example, gaze-following in long-tailed macaques increases when a human demonstrator

looks with a negative emotional facial expression that signals submission [35\*]. That this behavior is modulated by salient affective cues thus suggests that gaze-following may be most important for some species during specific social contexts, such as times of distress. Furthermore, in rhesus macaques gaze toward social partners appears to be modulated by rank [45]. As rhesus are notable for their despotic social hierarchy, one prediction is therefore that a more egalitarian species of macaques might show a different pattern of gaze-following in response to individuals of varying rank.

Finally, any adaptive explanation for a trait must ultimately show that the trait is both heritable and has a differential impact on reproductive success. This is a high bar to set for studies of slow-breeding primates, but evidence is accumulating that does bear on this issue. First, studies in the wild indicate that the quality of social relationships females have with group mates does impact the survival of their infants [46]. While there is as of yet no direct evidence that any particular social-cognitive ability *per se* impacts fitness, this is some of the first evidence that social competency plays an important role in primate reproductive success. Second, studies of domestication in canids indicate that it is possible to select for improved ability to utilize social cues like gaze [47]. Thus, gaze-following skills probably have a genetic basis that can be shaped by selective pressures, at least in some taxa. Finally, studies examining individual variance in the cognitive skills of primates will allow researchers to examine how gaze-following relates to other social-cognitive abilities [13], and provides a way to address variance in gaze-following both between and within species. For example, neither chimpanzees and orangutans show sex differences in their tendency to follow gaze, in contrast to evolutionary explanations for human sex differences [48,49] proposing that social information is more important for females. Examining sensitivity to gaze information across species, across contexts, and across individuals thus offers a productive avenue to explore the adaptive nature of these social-cognitive skills.

## Conclusion

Taken together, comparative studies of gaze-following in primates provide an important warning for the cognitive sciences: there is no such thing as ‘primate social cognition.’ Comparative research – although patchy – has increasingly revealed the diversity of primate social psychology, making it more appropriate to talk about ‘chimpanzee social cognition,’ ‘rhesus monkey social cognition,’ or ‘capuchin monkey social cognition’—some of the very few species that have been studied enough to make generalized claims about their psychology [50]. Such an emphasis on the *differences* between species quickly presents a serious challenge to research endeavors that use a few model species in hopes of understanding cognitive traits across wide phylogenetic spaces. While a

model systems approach has obviously been fruitful, it also has serious limitations. For instance, it is important to recognize that such an approach cannot be used to address ultimate questions about the origins and causes of traits—including cognitive skills. As all psychological mechanisms have evolved, and the course of evolution is constrained by pre-existing mechanisms in the brain, a complete understanding of social cognition will require that both the proximate and the ultimate levels are addressed. Thus, we hope that we have piqued interest as to what the causes and origins of social-cognitive mechanisms across primates might be.

## References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- of outstanding interest

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