

The evolutionary origins of natural pedagogy: Rhesus monkeys show sustained attention following nonsocial cues versus social communicative signals

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Abstract

The natural pedagogy hypothesis proposes that human infants preferentially attend to communicative signals from others, facilitating rapid cultural learning. In this view, sensitivity to such signals is a uniquely human adaptation and as such nonhuman animals should not produce or utilize these communicative signals. We test these evolutionary predictions by examining sensitivity to communicative cues in 206 rhesus monkeys (*Macaca mulatta*) using an expectancy looking time task modeled on prior work with infants. Monkeys observed a human actor who either made eye contact and vocalized to the monkey (*social cue*), or waved a fruit in front of her face and produced a tapping sound (*nonsocial cue*). The actor then either looked at an object (*referential look*) or looked toward empty space (*look away*). We found that, unlike human infants in analogous situations, rhesus monkeys looked longer at events following nonsocial cues, regardless of the demonstrator's subsequent looking behavior. Moreover younger and older monkeys showed similar patterns of responses across development. These results provide support for the natural pedagogy hypothesis, while also highlighting evolutionary changes in human sensitivity to communicative signals.

KEYWORDS

comparative development, gaze, pedagogy, primates, social cognition

1 | INTRODUCTION

One of the biggest challenges faced by any developing organism is to learn about the world around it. Social information provided by others can facilitate such learning, and human infants are highly sensitive to social cues that can help them acquire this information (Baldwin, 1993; Flom, Lee, & Muir, 2017; Meltzoff, Kuhl, Movellan, & Sejnowski, 2009; Tomasello, 2009). An influential hypothesis proposes that human infants are uniquely receptive to 'ostensive' social communicative cues, like directed gaze or infant-directed speech, which denote that information is being intentionally communicated (Csibra, 2010; Csibra & Gergely, 2009; Gergely & Csibra, 2006). While children can also learn new information even when it is not intentionally conveyed (Gredebäck, Astor, & Fawcett, 2018; Schmidt,

Rakoczy, & Tomasello, 2011), this proposal argues that communicative cues may enable especially efficacious social learning if infants preferentially attend to and interpret these communicative acts appropriately (Csibra, 2010; Gergely & Csibra, 2006; Moore, 2016; Sperber & Wilson, 1986). A key claim of the natural pedagogy hypothesis is that humans are uniquely adapted to produce and interpret these 'ostensive' cues which signal that important information is being conveyed, and thus facilitate cultural learning (Csibra, 2010; Csibra & Gergely, 2009; Gergely & Csibra, 2006). Here we test a key prediction of this proposal by examining whether rhesus monkeys are similarly sensitive to social communicative cues.

Empirical evidence testing this proposal indicates that human infants do attend to and interpret communicative signals in a way that facilitates social learning. First, infants *preferentially attend to*



cues such as eye contact or infant-directed speech, looking more at faces with direct gaze than averted gaze, and preferring infant-directed speech (Cooper & Aslin, 1990; Farroni, Csibra, Simion, & Johnson, 2002). Second, infants expect these signals to be followed by *referential information*. For example, infants are more likely to follow an experimenter's gaze following ostensive cues, compared to attention grabbing but nonsocial cues (Senju & Csibra, 2008). These signals appear to help the infants selectively attend to the referent (e.g. target object) that the adult is looking at. Similarly, in expectancy violation looking-time paradigms, infants look longer when an experimenter gives an ostensive cue and then fails to look at an object, compared to when the adult does look to an object (Csibra & Volein, 2008) – that is, they seem to expect that ostensive cues will be referential. Finally, infants infer that ostensive cues precede *generalizable information*, rather than applying only to the 'here-and-now' or to a particular person's preferences. For example, infants preferentially encode kind-relevant properties about an object following ostensive cues (Topál, Gergely, Miklósi, Erdőhegyi, & Csibra, 2008; Yoon, Johnson, & Csibra, 2008). These results support the claim that ostensive cues can enable cultural learning in humans – knowledge that should be generalizable across different people and contexts within a shared culture.

The natural pedagogy hypothesis specifically predicts that these patterns of social cue production and use are unique to humans, facilitating the novel patterns of cultural behavior seen in our species (Csibra & Gergely, 2009, 2011). In line with this, there is little evidence that animals *produce* these communicative signals. Nonhuman primates do have complex forms of vocal and gestural communication, some of which has been proposed reflect intentional communication (Byrne et al., 2017; Tomasello & Call, 2019; but see Fischer & Price, 2017). However, there is currently no clear evidence that nonhuman primate communication involves ostensive signals which specifically denotes the signaler's intent to communicate to the receiver, a crucial component of human-like communication (Csibra & Gergely, 2011; Grice, 1989). For example, while some animals may engage in behaviors that meet a functional, evolutionary definition of teaching focused on whether information is conveyed at a cost to the actor (Musgrave, Morgan, Lonsdorf, Mundry, & Sanz, 2016; Thornton & McAuliffe, 2006; Thornton & Raihani, 2008), there is no evidence that 'teachers' produce intentional communicative signals to facilitate learning.

However, some nonhumans may be *sensitive* to such cues, a potential precursor to human-like natural pedagogy. For example, dogs attend to eye contact and name-calling (Kaminski, Schulz, & Tomasello, 2012), and preferentially gaze follow to the referent object after the production of these cues (Téglás, Gergely, Kupán, Miklósi, & Topál, 2012). More generally, domesticated animals are fairly successful at following a human demonstrator's social cues, such as directed gaze or pointing (Bräuer, Kaminski, Riedel, Call, & Tomasello, 2006; Hare, Brown, Williamson, & Tomasello, 2002; Hare et al., 2005; Hare & Tomasello, 2005; Kaminski, Riedel, Call, & Tomasello, 2005). One explanation for these findings is that the process of dog domestication selected for cognitive abilities, such as

Research highlights

- Comparisons of nonhuman primate cognition can provide insights into the evolutionary roots of human social cognitive development
- We examined whether rhesus monkeys are sensitive to social communicative signals that are proposed to facilitate cultural learning in human infants
- Unlike humans, rhesus monkeys look longer following nonsocial cues and do not expect social cues to be followed by referential actions
- These results provide support for the natural pedagogy hypothesis, which argues that sensitivity to 'ostensive' cues is a uniquely human adaptation

interpreting human social cues, that facilitated living among humans (Hare, 2007, 2017; Hare & Tomasello, 2005). An important question is then whether nonhuman primates are sensitive to ostensive signals, given that primates are our closest evolutionary relatives. To date, only one study has tested the natural pedagogy hypothesis in primates (Kano et al., 2018). Chimpanzees, bonobos, and orangutans watched as a human demonstrator gave an ostensive cue or a nonsocial cue and then looked toward one of two objects, following methods used previously with infants (Senju & Csibra, 2008). In fact, apes did not preferentially follow the demonstrator's gaze to the cue object following the ostensive signals, although chimpanzees showed greater attention toward both objects following these signals. Thus, chimpanzees might attend to these cues, but fail to utilize gaze information to identify the intended referent. Notably, this study tested mostly adults, whereas the natural pedagogy hypothesis proposes that cue sensitivity is especially important for young individuals who must rapidly absorb social knowledge (Csibra, 2010; Csibra & Gergely, 2009; Gergely & Csibra, 2006). As such, a comparative developmental perspective is critical to testing this hypothesis (Gómez, 2005; Matsuzawa, 2007; Rosati, Wobber, Hughes, & Santos, 2014).

In the current work, we therefore examined sensitivity to social communicative cues in rhesus monkeys varying in age from juvenility to adulthood. Rhesus monkeys do not exhibit human-like culture, but have many similarities to humans in their social cognition, and therefore can provide an important test of whether humans have a unique sensitivity to these cues. For example, rhesus monkeys and humans exhibit similarities in gaze sensitivity. Like humans, macaque newborns engage in long bouts of mutual gaze and facial gesture imitation with their mother (Dettmer et al., 2016; Ferrari, Paukner, Ionica, & Suomi, 2009; Simpson, Miller, Ferrari, Suomi, & Paukner, et al., 2016). Rhesus monkeys also robustly follow others' gaze (Emery, Lorincz, Perrett, Oram, & Baker, 1997; Rosati & Santos, 2017; Tomasello, Hare, & Fogleman, 2001), with developmental trajectories mirroring those in humans (Rosati, Arre, Platt, & Santos, 2016; Tomasello et al., 2001). Macaques also have a rich vocal and gestural communication system comprising different vocalizations and expressions including screams in



agonistic contexts (Gouzoules, Gouzoules, & Marler, 1984; Maestriperi & Wallen, 1997), affiliative lip-smacking (Ferrari et al., 2009; Morrill, Paukner, Ferrari, & Ghazanfar, 2012; Simpson, Paukner, Sclafani, Suomi, & Ferrari, 2013), and grunts or threats (Maestriperi & Wallen, 1997; Partan, 2002).

Here, we tested a large sample ($n = 206$) of semi-free-ranging rhesus monkeys on a new expectancy looking-time paradigm integrating components of previous infant studies (Csibra & Volein, 2008; Senju & Csibra, 2008). In a between-subjects design, monkeys watched a demonstrator give either an ostensive signal (*social cue condition*; the demonstrator made directed eye contact and vocalized), or observed a salient but nonsocial cue (*nonsocial cue condition*; a fruit moved in front of the demonstrator's face concurrent with a mechanical knocking sound). Immediately following this cue, monkeys observed the demonstrator either look toward a location where an object was revealed (*look to object outcome*), or in the opposite direction to empty space (*look away outcome*). We tested if monkeys (a) preferentially watch events following social communicative cues; (b) expect communicative cues to be followed by referential actions; and (c) exhibit exacerbated sensitivity to such cues as juveniles. We predicted that if monkeys were sensitive to ostensive signals, they would show longer looking times following the social cue, especially when the demonstrator then produced the unexpected non-referential looking behavior. In contrast, the natural pedagogy hypothesis predicts that nonhumans will not prioritize such cues. Second, we predicted that if such signals facilitate social learning in monkeys, then juveniles should demonstrate enhanced sensitivity. In contrast, the natural pedagogy hypothesis predicts that this early sensitivity is a human-specific adaptation, in which case older monkeys may show greater skillfulness than younger ones through learning to preferentially attend to such social cues through direct experience with humans over their lifetime.

2 | METHODS

2.1 | Subjects

We tested 206 rhesus monkeys (51 or 52 per condition; 115 males and 91 females; 1.8 to 23.6 years old) at the Cayo Santiago Field Station (see Rawlins & Kessler, 1986). We tested 99 adults and 107 juveniles, age balanced across conditions. This free-ranging population is well-habituated to humans, as behavioral observations and cognitive tasks are regularly conducted with this population. Individuals can be identified through tattoos and ear notches. This population has successfully been tested in a number of looking-time paradigms testing different aspects of social cognition (Marticorena, Ruiz, Mukerji, Goddu, & Santos, 2011; Martin & Santos, 2014; Rosati, Arre, Platt, & Santos, 2018).

2.2 | Procedure and apparatus

Monkeys were randomly assigned to one of four conditions in a 2×2 design manipulating whether the monkey saw a *social* or *nonsocial*

cue, and whether the demonstrator subsequently *looked to object* or *looked away* from an object during the test trial. Monkeys saw a white stage (backdrop: 76 cm \times 51 cm; base: 76 cm \times 15 cm) with a front screen (76 cm \times 51 cm) that could be raised and lowered (see Figure 1 and Video S1). At the front were two smaller purple occluders (10 cm \times 10 cm) which could also be lowered to reveal an object (a plastic orange). A track in the stage (63 cm long) allowed the experimenter to manipulate the orange out of the monkey's view. Such fruit stimuli are highly interesting to the monkeys (De Petrillo & Rosati, 2019; Hughes & Santos, 2012; Marticorena et al., 2011; Martin & Santos, 2014).

Experimenter 1 (E1; the actor) first identified a calmly sitting monkey, then placed the apparatus approximately 2m away and knelt behind it. Experimenter 2 (E2; the cameraperson) knelt beside to film the monkey's looking responses. Both wore baseball caps to cover their eyes with the brim when necessary (see Figure 1). All monkeys first saw a *habituation trial* (identical across trials). E1 lowered the front screen then watched the fruit as it traveled behind each of the small occluders (see Figure 1). Once the fruit returned to the center, E1 called 'now' and looked down, and the monkey's looking was video-recorded for 10s. This habituation trial thus familiarized the monkey to the basic setup and the fact that the orange could move. After 10s, E2 called 'stop' and E1 raised the front occluder.

Next, the monkey observed the production of a cue followed by a test trial. In the *cue production phase*, the monkey either saw a *social cue* or a *nonsocial cue* (see Figure 1b). In the social cue, E1 made eye contact with the monkey and called out 'monkey, monkey!'. In the nonsocial cue, an apple popped up from behind the stage and moved in front of E1's face concurrent with a tapping sound. Importantly, the stage obscured E1's hands and arms such that the *nonsocial cues* were not visibly produced by E1: E1 could manipulate this apple out of the monkey's sight behind the stage, and the tapping sound was produced by surreptitiously knocking the back of the apparatus. This lasted approximately 3s; then the apple was removed. Next, E1 lowered the purple occluders to reveal the orange (the right side; see Figure 1c). Concurrent with this, she said 'now' and either looked toward the orange (*look to object*) or toward empty space (*look away*) in the *test trial*. The monkey's looking time was again recorded for 10s. Cue and trial outcome condition assignment was random, using a pre-designated list carried by E2; E1 was not told the condition until the trial started. The monkey never received any food reward in the task.

2.3 | Exclusions

In this free-ranging population, monkeys were sometimes approached but failed to complete the study (did not produce scorable responses). Reasons for exclusion included: disinterest and leaving the testing area ($n = 54$); interference by other monkeys ($n = 16$); approaching too close ($n = 8$); poor video quality ($n = 5$), or experimenter or equipment error ($n = 11$). This rate of aborted sessions ($n = 94$) is similar to other looking time tasks in this population (Marticorena

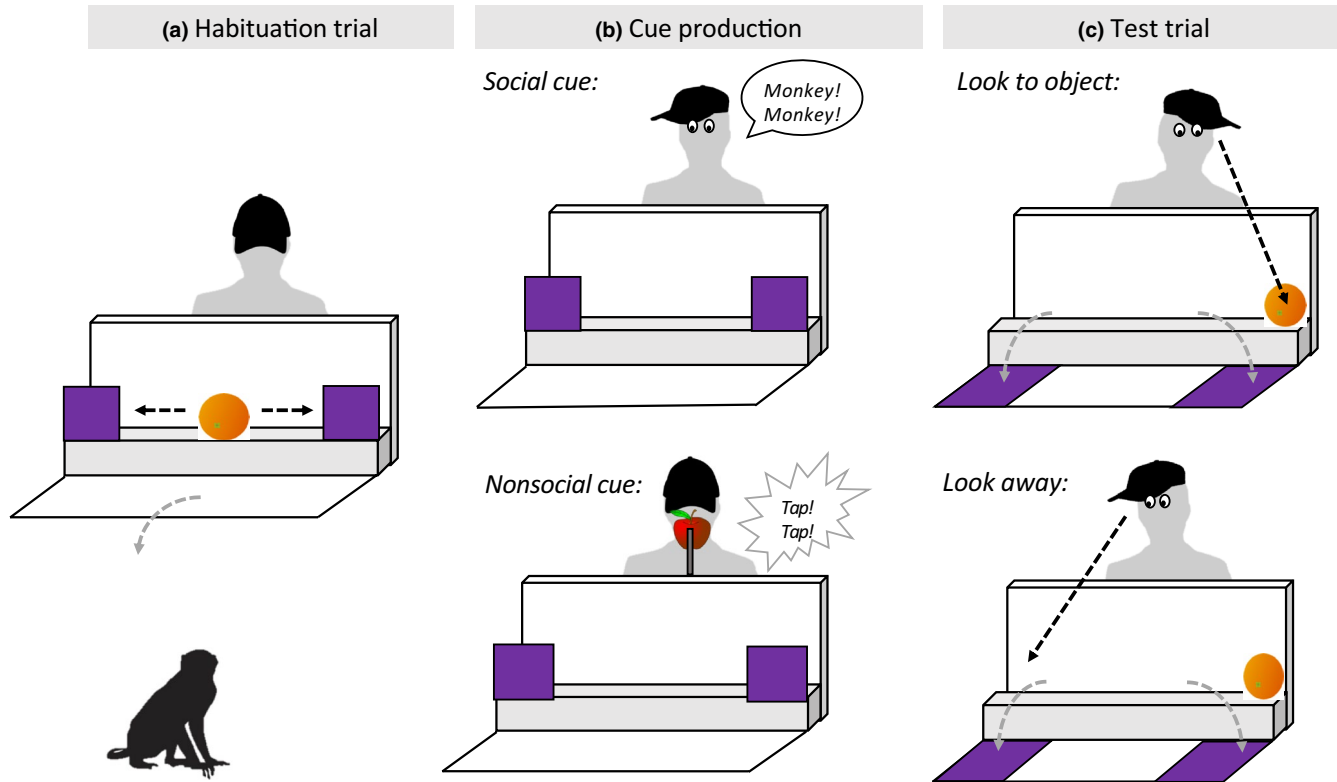


FIGURE 1 Setup and experimental procedure. In the (a) *habituation trial*, the occluder dropped to reveal an orange that moved back-and-forth behind both small purple occluders, before stopping in the center; E1 moved her head to follow the fruit's movements and said 'left box, right box' as the orange moved behind each occluder. She then called 'now' and looked down (obscuring her eyes with the cap) to initiate the trial. In the (b) *cue production* phase, monkeys either saw a demonstrator make eye contact and vocalize in the *social cue condition*, or saw an apple move in front of her face and heard a tapping sound in the *nonsocial cue condition*. E1 manipulated the stick and made the sound by tapping on the back of the apparatus, but this was not visible to the monkey because the stage obscured her hands and arms. The apple dropped behind the back of the apparatus at the end of this period. In the (c) *test trial*, monkeys saw both small purple occluders fall as the demonstrator either looked toward the revealed location of the orange (*look to object*), or looked toward empty space (*look away*)

et al., 2011; Martin & Santos, 2014). If a monkey was tested more than once (e.g. because they were only individually identified after the test: $n = 24$), we only coded and analyzed their first session.

2.4 | Video coding and reliability

Two coders blind to trial type and condition independently scored both trials from the final subjects. Each trial was clipped from longer video sessions and assigned a random trial ID to remove condition information. The coders examined these video clips frame-by-frame using MPEG Streamclip to assess total looking time per trial out of 10 s. There was high reliability between the two coders ($r_p = 0.92$).

2.5 | Statistical analyses

We analyzed the data in R v3.4.1 (R Development Core Team, 2019). Our primary analysis examined duration of looking across habituation and test trials using linear mixed models implemented with the *lmer* function in the package *lme4* (Bates, Mächler, Bolker, & Walker,

2015). In some analyses we further examined a difference score for each individual (Test looking time - Habituation looking time), which has commonly been used in looking time research with infants (Spelke, Breinlinger, Macomber, & Jacobson, 1992). To analyze these scores, we implemented linear regressions using the *lm* function. We compared model fit using likelihood ratio tests (Bolker et al., 2009). We accounted for sex in all models as prior work suggests that male and female rhesus monkeys can show different responses to social information (Rosati et al., 2016; Rosati & Santos, 2017; Simpson, Nicolini, et al., 2016). To examine age-related changes in responses, we compared age cohorts based on life history transitions, with juvenile less than 5 years of age (the onset of sexual maturity), and adults over age 5 (Bercovitch et al., 2003; Rawlins & Kessler, 1986; Rosati et al., 2016). We also performed additional checks using age in as a continuous predictor.

3 | RESULTS

We first examined monkeys' looking times to the habituation versus test trial across conditions. On average, monkeys looked

mean = $4.73 \pm \text{SE} = 0.20$ s in the habituation trial, but showed different patterns of looking to the test trial (see Figure 2). In particular, they looked relatively longer in test trials compared to habituation trials following nonsocial cues regardless of the actor's subsequent looking behavior (*look to object outcome*: 6.09 ± 0.32 s; paired samples *t* test comparing habituation to test: $t_{50} = 3.21$, $p = .002$; 95% CI of the mean difference = [0.43, 1.89]; *look away outcome*: 5.84 ± 0.35 s, $t_{51} = 4.76$, $p < .0001$, 95% CI = [1.05, 2.57]). However, they did not differ in their looking to test trials compared to habituation trials following social cues (*look to object outcome*: 5.58 ± 0.40 s; $t_{50} = 1.83$, $p = .07$, n.s., 95% CI = [-0.09, 1.84]; *look away outcome*: 5.24 ± 0.38 s, $t_{51} = -0.06$, $p = .95$, n.s., 95% CI = [-0.93, 0.88]). Thus, monkeys exhibited more sustained attention to the test events following the nonsocial cue.

To compare responses across conditions, we used linear mixed models accounting for *subject identity* (as a random effect); *sex*; *age cohort*; and *trial type* (habituation vs. test trial). In the second model, we added the interaction between *trial type* and *cue type* (social vs. nonsocial) and to test whether monkeys attended differentially to test depending on cue. This improved model fit [LRT: $\chi^2 = 6.38$, $df = 2$, $p = .04$]: monkeys looked longer following nonsocial but not social cues. This confirms that monkeys exhibited more sustained looking after nonsocial cues. In the third model, we additionally added the interaction between *trial type* and *test trial outcome* (look to object or look away), which did not further improve fit [LRT: $\chi^2 = 0.65$, $df = 2$, $p = .72$, n.s.]: monkeys did not modulate their looking according to

whether the look was referential. Finally, inclusion of the three-way interaction between *trial type*, *social cue*, and *test trial outcome* also did not improve model fit [LRT: $\chi^2 = 7.13$, $df = 4$, $p = .13$, n.s.]. Thus, the full model showed that monkeys looked longer following nonsocial cues, but did not adjust looking based on the actor's subsequent looking behavior (see ESM for parameters from the full model). In the final model males also looked overall longer than females and juveniles longer than adults, similar to prior results (De Petrillo & Rosati, 2019; Hughes & Santos, 2012). Finally, we ran a similar analysis where we examined test trial responses while controlling for each individual's habituation looking time, and also found that monkeys looked longer following nonsocial cues (see ESM for details).

We next examined monkeys' difference scores (Test - Habituation Looking) to parse age-related change in patterns of relative looking across condition. Both younger and older monkeys had more positive scores following nonsocial cues (*juveniles*: 1.27 ± 0.38 s; *adults*: 1.72 ± 0.36 s; see Figure 3) compared to social cues (*juveniles*: 0.08 ± 0.46 s; *adults*: 0.80 ± 0.47 s). To analyze this, we first created a base linear model that included each subject's *cohort* and *sex*. We then added *cue type*, which improved model fit [LRT: $\chi^2 = 6.46$, $df = 1$, $p = .01$]: monkeys show more relative looking following nonsocial cues. Next, we added *test trial outcome*, which did not improve model fit [LRT: $\chi^2 = 0.13$, $df = 1$, $p = .72$, n.s.]. Finally, in the full model, we included a three-way interaction between *age cohort*, *cue type*, and *test trial outcome* to test whether differential responses to social cues and referential looking varied over development. This also did not

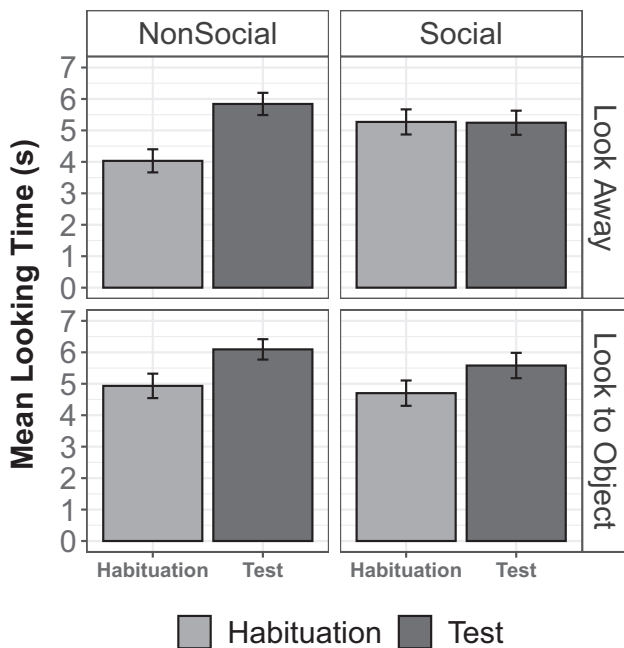


FIGURE 2 Looking responses across habituation and test trials depending on cue and looking outcome. After an initial habituation trial (identical for all conditions), monkeys experienced either a *social cue* or *nonsocial cue*, and then observed an actor either *look to an object* (referential look) or *look away* in the test trial. Looking times show duration of looking in seconds out of a possible total 10s; error bars indicate SE

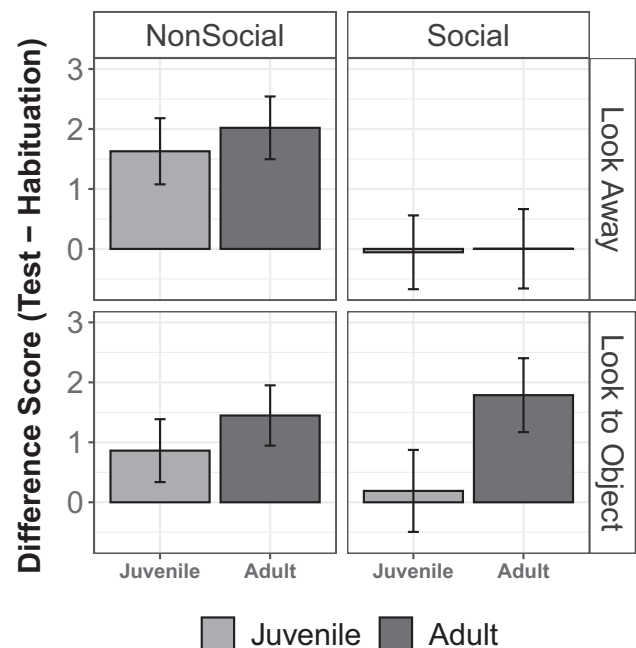


FIGURE 3 Relative patterns of looking over development. Both younger and older monkeys showed similar increases in looking to the test events following nonsocial cues as indexed by more positive looking time difference scores (Test Looking - Habituation Looking). In contrast, both age groups showed lower difference scores following social cues. Error bars indicate SE



improve model fit [LRT: $\chi^2 = 5.81$, $df = 5$, $p = .33$, n.s.]. That is, while younger monkeys did look longer overall at events (as indicated by the prior analyses of looking duration), they did not show a differential pattern of relative looking across conditions compared to older monkeys. Additional checks using age in years as a continuous predictor found largely similar results (see ESM for details).

4 | DISCUSSION

We tested comparative predictions from the natural pedagogy hypothesis by assessing how rhesus monkeys respond to communicative social signals and interpret subsequent looking behaviors by an actor. We found three key results. First, rhesus monkeys showed more sustained attention to events after nonsocial cues compared to social, communicative cues. Second, monkeys did not differentiate between a referential look to an object and a look to empty space – even though the referential cues signaled the location of a food item, an ecologically important type of information for primates. Finally, we compared these responses across the lifespan in the first comparative developmental study of primate responses to ostensive cues, and found no evidence that monkeys show lifespan changes in their sensitivity to these signals.

These results indicate that monkeys exhibit important differences in responsivity to social cues compared to human infants. First, monkeys attend more to events following nonsocial cues, whereas human infants are more likely to follow an adult's gaze following social cues specifically (Senju & Csibra, 2008), and generally find social communicative signals extremely salient (e.g. Baron-Cohen, 1997; Flom et al., 2017; Grossmann et al., 2008; Hood, Willen, & Driver, 1998). Second, monkeys looked longer after non-social cues regardless of whether the actor produced a referential look. In contrast, human infants are surprised when the adult gives a social cue and fails to subsequently look toward an object (Csibra & Volein, 2008; Wu & Kirkham, 2010). These differences suggest that monkeys are not sensitive to the communicative function of gaze the way humans are, even though they are responsive to shifts in a human's or a conspecific's gaze direction (Bettle & Rosati, 2019; Emery et al., 1997; Flombaum & Santos, 2005; Rosati et al., 2016; Rosati & Santos, 2017; Tomasello et al., 2001). Overall, these findings provide a new line of support for the natural pedagogy hypothesis, which argues that sensitivity to ostensive cues is unique to humans (Csibra, 2010; Csibra & Gergely, 2009; Gergely & Csibra, 2006). This further suggests that while some domesticates, like dogs, might be sensitive to such human communicative cues, this sensitivity may have evolved independently in response to the domestication process (Hare et al., 2002; Topál, Gergely, Erdőhegyi, Csibra, & Miklósi, 2009).

In this study, we also examined whether younger monkeys show greater sensitivity to social cues than older monkeys. The natural pedagogy hypothesis highlights that ostensive signals are especially important for learning in infancy (Csibra, 2010; Csibra & Gergely, 2009; Gergely & Csibra, 2006), yet to date no work has

tested whether juvenile animals are specifically responsive to these cues. Despite our large sample of both juvenile and adult monkeys, we did not find evidence for developmental change in responses to social cues. While younger monkeys exhibited longer looking times to various kinds of stimuli in general, as in prior work (De Petrillo & Rosati, 2019; Hughes & Santos, 2012; Rosati et al., 2018), they did not show different pattern of relative looking across conditions compared to adults. This suggests that juvenile monkeys do not prioritize ostensive cues the way human infants do (Csibra, 2010; Csibra & Gergely, 2009; Gergely & Csibra, 2006). Moreover the lack of lifespan developmental change also suggests that older monkeys did not learn to utilize the human-produced social cues through direct experience that such cues may predict that a human is looking at something interesting.

One possibility is that monkeys might be sensitive to other kinds of individuals, such as conspecifics, given that we used a human demonstrator in order to tightly control the actor's actions in the experiment. However, there are several reasons that this cannot explain our results. First, macaques follow the gaze of humans and conspecifics at similar rates, suggesting that human-produced gaze cues are interesting and relevant to them (Rosati & Santos, 2016, 2017; Tomasello et al., 2001). Indeed, a variety of results indicate that macaques utilize sophisticated social cognitive processes in their interactions with humans, and most evidence for these abilities in nonhumans comes from studies involving human actors (Bettle & Rosati, 2019; Drayton & Santos, 2017; Flombaum & Santos, 2005; Marticorena et al., 2011; Martin & Santos, 2014; Santos, Nissen, & Ferrugia, 2006). It is also possible that macaques might be more sensitive to other kinds of social cues than those used here. While the monkeys showed similar looking responses following the directed eye contact and vocalization cues as they did in the habituation trial without such cues, suggesting that they did not actively look away from the human social signals, other species-specific signals may be more relevant to them. For example, macaques use affiliative signals such as lip-smacking (Morrill et al., 2012; Simpson et al., 2013) and vocalizations such as grunts and girneys (Partan, 2002), which may be similar in function to directed gaze and infant-direct speech in humans.

Relatedly, nonhuman primates might selectively respond to communicative cues produced by specific individuals that they have a close, tolerant relationship with. For example, mother-infant monkey dyads engage in reciprocal lip-smacking and mutual gaze (Ferrari et al., 2009), which may serve to establish a mutual intent to communicate. In addition, chimpanzees are more sensitive to social cues from a human caregiver with whom they have a close relationship (Kano et al., 2018). In that way, social tolerance may promote communication between individuals who would otherwise avoid or even antagonise the other. A critical next step is therefore to examine whether more tolerant primate species exhibit enhanced sensitivity to social communicative cues, such as Barbary macaques (Almeling, Hammerschmidt, Sennhenn-Reulen, Freund, & Fischer, 2016; Rosati & Santos, 2017; Teufel, Gutmann, Pirow, & Fischer, 2010; Thierry, 2000). In humans,



higher levels of social tolerance has been proposed to facilitate new forms of cooperation and communications (Hare, 2017; Hare & Tomasello, 2005), so examining how more socially tolerant species respond to these signals is important for assessing the natural pedagogy hypothesis as well.

In conclusion, our work shows that monkeys across the lifespan preferentially attended to events following nonsocial cues compared to social communicative signals, and did not exhibit referential expectations that a look to an object will follow these cues. This supports the proposal that sensitivity to social signals may facilitate a novel cultural learning function in humans (Csibra & Gergely, 2009; Gergely & Csibra, 2006; Kaplan, Lancaster, & Robson, 2003). Human children are unique in terms of the volume of culturally specific and cognitively opaque information they need to learn, which means that the information human children must absorb is difficult to learn via other learning processes that are more widely shared across species. This human-specific ability to intentionally transmit complex cultural knowledge may also be impossible without the extensive cooperation present in humans (Tennie, Call, & Tomasello, 2009). Our results therefore highlight the evolutionary changes in social cognition that may have occurred to support our species' shift toward increasing dependence upon cultural learning.

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DATA AVAILABILITY STATEMENT

All data from this study is available at Dryad Digital Repository (<https://doi.org/10.5061/dryad.kwh70rz1h>).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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