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

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9 Research highlights

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

18 **Abstract**

19 The natural pedagogy hypothesis proposes that human infants preferentially attend to
20 communicative signals from others, facilitating rapid cultural learning. In this view, sensitivity to
21 such signals are a uniquely human adaptation and as such nonhuman animals should not produce
22 or utilize these communicative signals. We test these evolutionary predictions by examining
23 sensitivity to communicative cues in 208 rhesus monkeys (*Macaca mulatta*) using an expectancy
24 looking time task modeled on prior work with infants. Monkeys observed a human actor who
25 either made eye contact and vocalized to the monkey (*social cue*), or waved a fruit in front of her

26 face and produced a tapping sound (*nonsocial cue*). The actor then either looked at an object
27 (*referential look*) or looked towards empty space (*look away*). We found that, unlike human
28 infants in analogous situations, rhesus monkeys looked longer at events following nonsocial
29 cues, regardless of the demonstrator's subsequent looking behavior. Moreover, younger and
30 older monkeys showed similar patterns of responses across development. These results provide
31 support for the natural pedagogy hypothesis, while also highlighting evolutionary changes in
32 human sensitivity to communicative signals.

33
34 **Keywords:**

35 Primates, social cognition, comparative development, gaze, pedagogy
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41 **Introduction**

42 One of the biggest challenges faced by any developing organism is to learn about the
43 world around it. Social information provided by others can facilitate such learning, and human
44 infants are highly sensitive to social cues that can help them acquire this information (Baldwin,
45 1993; Flom et al., 2017; Meltzoff et al., 2009; Tomasello, 2009). An influential hypothesis
46 proposes that human infants are uniquely receptive to 'ostensive' social communicative cues,
47 like directed gaze or infant-directed speech, which denote that information is being intentionally
48 communicated (Csibra, 2010; Csibra & Gergely, 2009; Gergely & Csibra, 2006). While children
49 can also learn new information even when it is not intentionally conveyed (Gredebäck et al.,
50 2018; Schmidt et al., 2011), this proposal argues that communicative cues may enable especially
51 efficacious social learning if infants preferentially attend to and interpret these communicative
52 acts appropriately (Csibra, 2010; Gergely & Csibra, 2006; Moore, 2016; Sperber & Wilson,
53 1986). A key claim of the natural pedagogy hypothesis is that humans are uniquely adapted to
54 produce and interpret these 'ostensive' cues which signal that important information is being
55 conveyed, and thus facilitate cultural learning (Csibra, 2010; Csibra & Gergely, 2009; Gergely &

56 Csibra, 2006). Here we test a key prediction of this proposal by examining whether rhesus
57 monkeys are similarly sensitive to social communicative cues.

58 Empirical evidence testing this proposal indicates that human infants do attend to and
59 interpret communicative signals in a way that facilitates social learning. First, infants
60 *preferentially attend* to cues such as eye contact or infant-directed speech, looking more at faces
61 with direct gaze than averted gaze, and preferring infant-directed speech (Cooper & Aslin, 1990;
62 Farroni et al., 2002). Second, infants expect these signals to be followed by *referential*
63 *information*. For example, infants are more likely to follow an experimenter's gaze following
64 ostensive cues, compared to attention-grabbing but nonsocial cues (Senju & Csibra, 2008).
65 These signals appear to help the infants selectively attend to the referent (e.g., target object) that
66 the adult is looking at. Similarly, in expectancy violation looking-time paradigms, infants look
67 longer when an experimenter gives an ostensive cue and then fails to look at an object, compared
68 to when the adult does look to an object (Csibra & Volein, 2008)—that is, they seem to expect
69 that ostensive cues will be referential. Finally, infants infer that ostensive cues precede
70 *generalizable information*, rather than applying only to the 'here-and-now' or to a particular
71 person's preferences. For example, infants preferentially encode kind-relevant properties about
72 an object following ostensive cues (Yoon et al., 2008, Topál et al., 2008). These results support
73 the claim that ostensive cues can enable cultural learning in humans—knowledge that should
74 be generalizable across different people and contexts within a shared culture.

75 The natural pedagogy hypothesis specifically predicts that these patterns of social cue
76 production and use are unique to humans, facilitating the novel patterns of cultural behavior seen
77 in our species (Csibra & Gergely, 2009; Csibra & Gergely, 2011). In line with this, there is little
78 evidence that animals *produce* these communicative signals. Nonhuman primates do have
79 complex forms of vocal and gestural communication, some of which has been proposed reflect
80 intentional communication (Byrne et al., 2017; Tomasello & Call, 2019; but see Fischer & Price,
81 2017). However, there is currently no clear evidence that non-human primate communication
82 involves ostensive signals which specifically denotes the signaler's intent to communicate to the
83 receiver, a crucial component of human-like communication (Csibra & Gergely, 2011; Grice,
84 1989). For example, while some animals may engage in behaviors that meet a functional,
85 evolutionary definition of teaching focused on whether information is conveyed at a cost to the

86 actor (Musgrave et al., 2016; Thornton & McAuliffe, 2006; Thornton & Raihani, 2008), there is
87 no evidence that ‘teachers’ produce intentional communicative signals to facilitate learning.

88 However, some nonhumans may be *sensitive* to such cues, a potential precursor to
89 human-like natural pedagogy. For example, dogs attend to eye contact and name-calling
90 (Kaminski et al., 2012), and preferentially gaze follow to the referent object after the production
91 of these cues (Téglás et al., 2012). More generally, domesticated animals are fairly successful at
92 following a human demonstrator’s social cues, such as directed gaze or pointing (Bräuer et al.,
93 2006; Hare et al., 2002; Hare et al., 2005; Hare & Tomasello, 2005; Kaminski et al., 2005). One
94 explanation for these findings is that the process of dog domestication selected for cognitive
95 abilities, such as interpreting human social cues, that facilitated living amongst humans (Hare,
96 2007, 2017; Hare & Tomasello, 2005). An important question is then whether nonhuman
97 primates are sensitive to ostensive signals, given that primates are our closest evolutionary
98 relatives. To date, only one study has tested the natural pedagogy hypothesis in primates (Kano
99 et al., 2018). Chimpanzees, bonobos, and orangutans watched as a human demonstrator gave an
100 ostensive cue or a nonsocial cue and then looked towards one of two objects, following methods
101 used previously with infants (Senju & Csibra, 2008). In fact, apes did not preferentially follow
102 the demonstrator’s gaze to the cue object following the ostensive signals, although chimpanzees
103 showed greater attention towards both objects following these signals. Thus, chimpanzees might
104 attend to these cues, but fail to utilize gaze information to identify the intended referent. Notably,
105 this study tested mostly adults, whereas the natural pedagogy hypothesis proposes that cue
106 sensitivity is especially important for young individuals who must rapidly absorb social
107 knowledge (Csibra, 2010; Csibra & Gergely, 2009; Gergely & Csibra, 2006). As such, a
108 comparative developmental perspective is critical to testing this hypothesis (Gómez et al., 2005;
109 Matsuzawa et al., 2007; Rosati et al., 2014).

110 In the current work, we therefore examined sensitivity to social communicative cues in
111 rhesus monkeys varying in age from juvenility to adulthood. Rhesus monkeys do not exhibit
112 human-like culture, but have many similarities to humans in their social cognition, and therefore
113 can provide an important test of whether humans have a unique sensitivity to these cues. For
114 example, rhesus monkeys and humans exhibit similarities in gaze sensitivity. Like humans,
115 macaque newborns engage in long bouts of mutual gaze and facial gesture imitation with their
116 mother (Dettmer et al., 2016; Ferrari et al., 2009; Simpson et al., 2016). Rhesus also robustly

117 follow others' gaze (Emery et al., 1997; Rosati & Santos, 2017; Tomasello et al., 2001), with
118 developmental trajectories mirroring those in humans (Rosati et al., 2016; Tomasello et al.,
119 2001). Macaques also have a rich vocal and gestural communication system comprising
120 different vocalizations and expressions including screams in agonistic contexts (Gouzoules et al.,
121 1984; Maestripieri & Wallen, 1997), affiliative lip-smacking (Ferrari et al., 2009; Morrill et al.,
122 2012; Simpson et al., 2013), and grunts or threats (Partan et al., 2002; Maestripieri & Wallen,
123 1997).

124 Here, we tested a large sample (n = 208) of semi-free-ranging rhesus monkeys on a new
125 expectancy looking-time paradigm integrating components of previous infant studies (Csibra &
126 Volein, 2008; Senju & Csibra, 2008). In a between-subjects design, monkeys watched a
127 demonstrator give either an ostensive signal (*social cue condition*; the demonstrator made
128 directed eye contact and vocalized), or observed a salient but nonsocial cue (*nonsocial cue*
129 *condition*; a fruit moved in front of the demonstrator's face concurrent with a mechanical
130 knocking sound). Immediately following this cue, monkeys observed the demonstrator either
131 look towards a location where an object was revealed (*look to object outcome*), or in the opposite
132 direction to empty space (*look away outcome*). We tested if monkeys (1) preferentially watch
133 events following social communicative cues; (2) expect communicative cues to be followed by
134 referential actions; and (3) exhibit exacerbated sensitivity to such cues as juveniles. We predicted
135 that if monkeys were sensitive to ostensive signals, they would show longer looking times
136 following the social cue, especially when the demonstrator then produced the unexpected non-
137 referential looking behavior. In contrast, the natural pedagogy hypothesis predicts that
138 nonhumans will not prioritize such cues. Second, we predicted that if such signals facilitate
139 social learning in monkeys, then juveniles should demonstrate enhanced sensitivity. In contrast,
140 the natural pedagogy hypothesis predicts that this early sensitivity is a human-specific adaption,
141 in which case older monkeys may show greater skillfulness than younger ones through learning
142 to preferentially attend to such social cues through direct experience with humans over their
143 lifetime.

144

145 **Methods**

146 *Subjects*

147 We tested 208 rhesus monkeys (52 per condition; 89 males and 119 females; 1.7 to 23.4
148 years old) at the Cayo Santiago Field Station (see Rawlins & Kessler, 1986). We tested 100
149 adults and 108 juveniles, age balanced across conditions. This free-ranging population is well-
150 habituated to humans, as behavioral observations and cognitive tasks are regularly conducted
151 with this population. Individuals can be identified through tattoos and ear notches. This
152 population has successfully been tested in a number of looking-time paradigms testing different
153 aspects of social cognition (Marticorena et al., 2011; Martin & Santos, 2014; Rosati et al., 2018).

154

155 *Procedure and apparatus*

156 Monkeys were randomly assigned to one of four conditions in a 2x2 design manipulating
157 whether the monkey saw a *social* or *nonsocial cue*, and whether the demonstrator subsequently
158 *looked to object* or *looked away* from an object during the test trial. Monkeys saw a white stage
159 (backdrop: 76cm x 51cm; base: 76cm x 15cm) with a front screen (76cm x 51cm) that could be
160 raised and lowered (see Figure 1 and Video S1). At the front were two smaller purple occluders
161 (10cm x 10cm) which could also be lowered to reveal an object (a plastic orange). A track in the
162 stage (63 cm long) allowed the experimenter to manipulate the orange out of the monkey's view.
163 Such fruit stimuli are highly interesting to the monkeys (De Petrillo & Rosati, 2019; Hughes &
164 Santos, 2012; Marticorena et al., 2011; Martin & Santos, 2014)

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

174 Next, the monkey observed the production of a cue followed by a test trial. In the *cue*
175 *production phase*, the monkey either saw a *social cue* or a *nonsocial cue* (see Figure 1b). In the
176 social cue, E1 made eye contact with the monkey and called out 'monkey, monkey!'. In the
177 nonsocial cue, an apple popped up from behind the stage and moved in front of E1's face

178 concurrent with a tapping sound. Importantly, the stage obscured E1's hands and arms such that
179 the *nonsocial cues* were not visibly produced by E1: E1 could manipulate this apple out of the
180 monkey's sight behind the stage, and the tapping sound was produced by surreptitiously
181 knocking the back of the apparatus. This lasted approximately 3s; then the apple was removed.
182 Next, E1 lowered the purple occluders to reveal the orange (the right side; see Figure 1c).
183 Concurrent with this, she said "now" and either looked towards the orange (*look to object*) or
184 towards empty space (*look away*) in the *test trial*. The monkey's looking time was again
185 recorded for 10s. Cue and trial outcome condition assignment was random, using a pre-
186 designated list carried by E2; E1 was not told the condition until the trial started. The monkey
187 never received any food reward in the task.

188

189 *Exclusions*

190 In this free-ranging population, monkeys were sometimes approached but failed to
191 complete the study (did not produce scorable responses). Reasons for exclusion included:
192 disinterest and leaving the testing area (n=54); interference by other monkeys (n=16);
193 approaching too close (n=8); poor video quality (n=5), or experimenter or equipment error
194 (n=11). This rate of aborted sessions (n=94) is similar to other looking time tasks in this
195 population (Marticorena et al., 2011; Martin & Santos, 2014). If a monkey was tested more than
196 once (e.g., because they were only individually identified after the test: n=22), we only coded
197 and analyzed their first session.

198

199 *Video coding and reliability*

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

205

206 *Statistical analyses*

207 We analyzed the data in R v3.4.1 (R Development Core Team, 2019). Our primary
208 analysis examined duration of looking across habituation and test trials using linear mixed

209 models implemented with the *lmer* function in the package lme4 (Bates et al. 2015). In some
210 analyses we further examined a difference score for each individual (Test looking time –
211 Habituation looking time), which has commonly been used in looking time research with infants
212 (Spelke et al., 1992). To analyze these scores, we implemented linear regressions using the *lm*
213 function. We compared model fit using likelihood ratio tests (Bolker et al., 2009). We accounted
214 for sex in all models as prior work suggests that male and female rhesus monkeys can show
215 different responses to social information (Rosati et al., 2016; Rosati & Santos 2017; Simpson et
216 al., 2016). To examine age-related changes in responses, we compared age cohorts based on life
217 history transitions, with juvenile less than 5 years of age (the onset of sexual maturity), and
218 adults over age 5 (Bercovitch et al. 2003; Rosati et al. 2016; Rawlins & Kessler 1986). We also
219 performed additional checks using age in as a continuous predictor.

220

221 **Results**

222 We first examined monkeys' looking times to the habituation versus test trial across
223 conditions. On average, monkeys looked mean = 4.77 ± SE = 0.20s in the habituation trial, but
224 showed different patterns of looking to the test trial (see Figure 2). In particular, they looked
225 relatively longer in test trials compared to habituation trials following nonsocial cues regardless
226 of the actor's subsequent looking behavior (*look to object outcome*: 6.16±0.33s; paired samples
227 t-test comparing habituation to test: $t_{51}=3.34$, $p=0.002$; 95% CI of the mean difference = [0.47,
228 1.90]; *look away outcome*: 5.84±0.35s, $t_{51}=4.76$, $p<0.0001$, 95% CI = [1.05, 2.57]). However,
229 they did not differ in their looking to test trials compared to habituation trials following social
230 cues (*look to object outcome*: 5.59±0.40s; $t_{51}= 1.64$, $p=0.11$, n.s., 95% CI = [-0.17, 1.75]; *look*
231 *away outcome*: 5.24±0.38s, $t_{51}=-0.06$, $p = 0.95$, n.s., 95% CI = [-0.93, 0.88]). Thus, monkeys
232 exhibited more sustained attention to the test events following the nonsocial cue.

233 To compare responses across conditions, we used linear mixed models accounting for
234 *subject identity* (as a random effect); *sex*; *age cohort*; and *trial type* (habituation versus test trial).
235 In the second model, we added the interaction between *trial type* and *cue type* (social versus
236 nonsocial) and to test whether monkeys attended differentially to test depending on cue. This
237 improved model fit [LRT: $\chi^2=7.11$, $df=2$, $p=0.03$]: monkeys looked longer following nonsocial
238 but not social cues. This confirms that monkeys exhibited more sustained looking after nonsocial
239 cues. In the third model, we additionally added the interaction between *trial type* and *test trial*

240 *outcome* (look to object or look away), which did not further improve fit [LRT: $\chi^2=0.63$, $df=2$,
241 $p=0.73$, n.s.]: monkeys did not modulate their looking according to whether the look was
242 referential. Finally, inclusion of the three-way interaction between *trial type*, *social cue*, and *test*
243 *trial outcome* also did not improve model fit [LRT: $\chi^2=6.38$, $df=4$, $p=0.17$, n.s.]. Thus, the full
244 model showed that monkeys looked longer following non-social cues, but did not adjust looking
245 based on the actor's subsequent looking behavior (see ESM for parameters from the full model).
246 In the final model males also looked overall longer than females and juveniles longer than adults,
247 similar to prior results (De Petrillo & Rosati, 2019; Hughes & Santos, 2012). Finally, we ran a
248 similar analysis where we examined test trial responses while controlling for each individual's
249 habituation looking time, and also found that monkeys looked longer following nonsocial cues
250 (see ESM for details).

251
252 We next examined monkeys' difference scores (Test – Habituation Looking) to parse
253 age-related change in patterns of relative looking across condition. Both younger and older
254 monkeys had more positive scores following nonsocial cues (*juveniles*: $1.21\pm 0.37s$; *adults*:
255 $1.80\pm 0.36s$; see Figure 3) compared to social cues (*juveniles*: $0.00\pm 0.46s$; *adults*: $0.80\pm 0.47s$).
256 To analyze this, we first created a base linear model that included each subject's *cohort* and *sex*.
257 We then added *cue type*, which improved model fit [LRT: $\chi^2=7.08$, $df=1$, $p=0.008$]: monkeys
258 show more relative looking following nonsocial cues. Next, we added *test trial outcome*, which
259 did not improve model fit [LRT: $\chi^2=0.09$, $df=1$, $p=0.76$, n.s.]. Finally, in the full model, we
260 included a 3-way interaction between *age cohort*, *cue type*, and *test trial outcome* to test whether
261 differential responses to social cues and referential looking varied over development. This also
262 did not improve model fit [LRT: $\chi^2=5.60$, $df=5$, $p=0.35$, n.s.]. That is, while younger monkeys
263 did look longer overall at events (as indicated by the prior analyses of looking duration), they did
264 not show a differential pattern of relative looking across conditions compared to older monkeys.
265 Additional checks using age in years as a continuous predictor found largely similar results (see
266 ESM for details).

267

268 **Discussion**

269 We tested comparative predictions from the natural pedagogy hypotheses by assessing
270 how rhesus monkeys respond to communicative social signals and interpret subsequent looking

271 behaviors by an actor. We found three key results. First, rhesus monkeys showed more sustained
272 attention to events after non-social cues compare to social, communicative cues. Second,
273 monkeys did not differentiate between a referential look to an object and a look to empty
274 space—even though the referential cues signaled the location of a food item, an ecologically
275 important type of information for primates. Finally, we compared these responses across the
276 lifespan in the first comparative developmental study of primate responses to ostensive cues, and
277 found no evidence that monkeys show lifespan changes in their sensitivity to these signals.

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

295 In the current work, we also examined whether younger monkeys show greater sensitivity
296 to social cues than older monkeys. The natural pedagogy hypothesis highlights that ostensive
297 signals are especially important for learning in infancy (Csibra, 2010; Csibra & Gergely, 2009;
298 Gergely & Csibra, 2006), yet to date no work has tested whether juvenile animals are specifically
299 responsive to these cues. Despite our large sample of both juvenile and adult monkeys, we did
300 not find evidence for developmental change in responses to social cues. While younger monkeys
301 exhibited longer looking times to various kinds of stimuli in general, as in prior work (De

302 Petrillo & Rosati, 2019; Hughes & Santos, 2012; Rosati et al., 2018), they did not show different
303 pattern of relative looking across conditions compared to adults. This suggests than juvenile
304 monkeys do not prioritize ostensive cues the way human infants do (Csibra, 2010; Csibra &
305 Gergely, 2009; Gergely & Csibra, 2006). Moreover, the lack of lifespan developmental change
306 also suggests that older monkeys did not learn to utilize the human-produced social cues through
307 direct experience that such cues may predict that a human is looking at something interesting.

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

325 Relatedly, nonhuman primates might selectively respond to communicative cues
326 produced by specific individuals that they have a close, tolerant relationship with. For example,
327 mother-infant monkey dyads engage in reciprocal lip-smacking and mutual gaze (Ferrari et al.,
328 2009), which may serve to establish a mutual intent to communicate. In addition, chimpanzees
329 are more sensitive to social cues from a human caregiver with whom they have a close
330 relationship (Kano et al., 2018). In that way, social tolerance may promote communication
331 between individuals who would otherwise avoid or even antagonise the other. A critical next step
332 is therefore to examine whether more tolerant primate species exhibit enhanced sensitivity to

333 social communicative cues, such as Barbary macaques (Almeling et al., 2016; Rosati & Santos,
334 2017; Teufel et al., 2010; Thierry, 2000). In humans, higher levels of social tolerance has been
335 proposed to facilitate new forms of cooperation and communications (Hare, 2017; Hare &
336 Tomasello, 2005), so examining how more socially tolerant species response to these signals is
337 important for assessing the natural pedagogy hypothesis as well.

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

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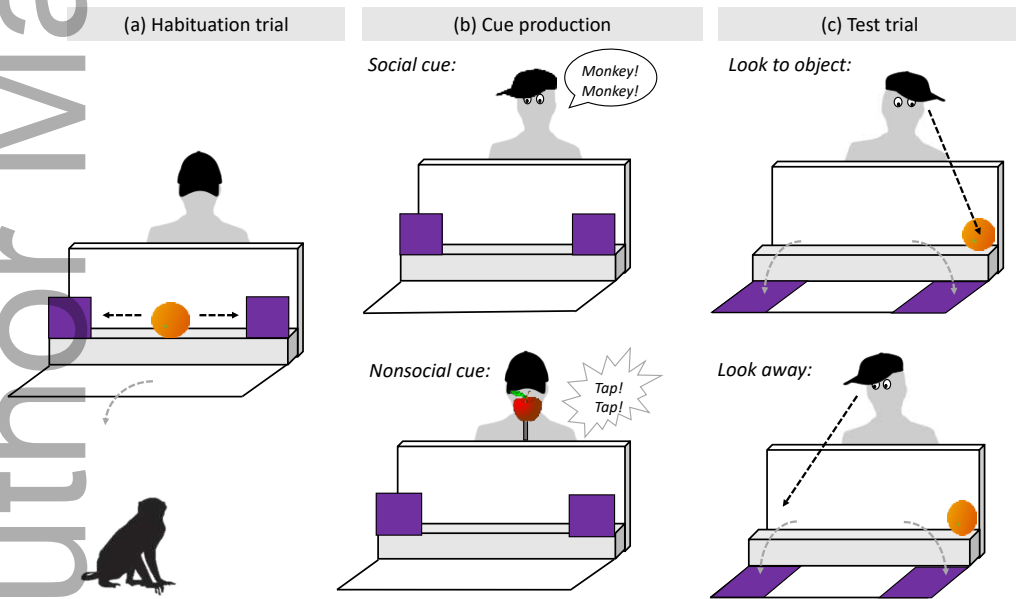
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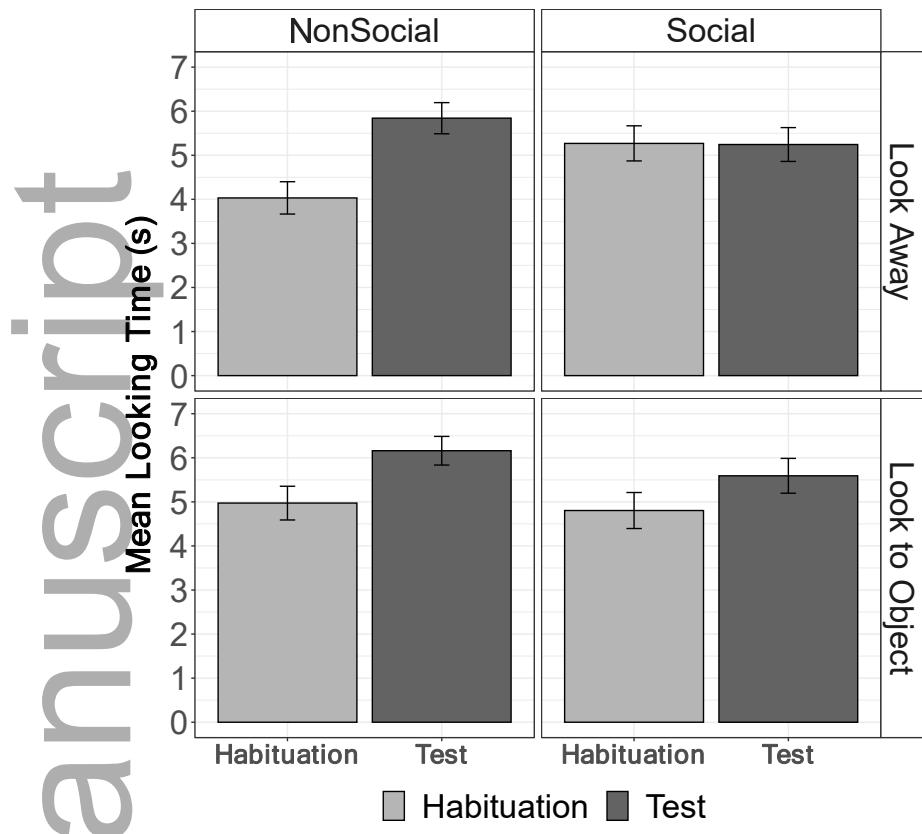
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Figure 1: Setup and experimental procedure. In the (a) *habituation trial*, the occluder dropped to reveal an orange that moved back-and-forth behind both small purple occluders, before stopping in the center; E1 moved her head to follow the fruit’s movements and said ‘left box, right box’ as the orange moved

598 behind each occluder. She then called ‘now’ and looked down (obscuring her eyes
599 with the cap) to initiate the trial. In the (b) *cue production* phase, monkeys either
600 saw a demonstrator make eye contact and vocalize in the *social cue condition*, or
601 saw an apple move in front of her face and heard a tapping sound in the *nonsocial*
602 *cue condition*. E1 manipulated the stick and made the sound by tapping on the
603 back of the apparatus, but this was not visible to the monkey because the stage
604 obscured her hands and arms. The apple dropped behind the back of the apparatus
605 at the end of this period. In the (c) test trial, monkeys saw both small purple
606 occluders fall as the demonstrator either looked towards the revealed location of
607 the orange (*look to object*), or looked towards empty space (*look away*).

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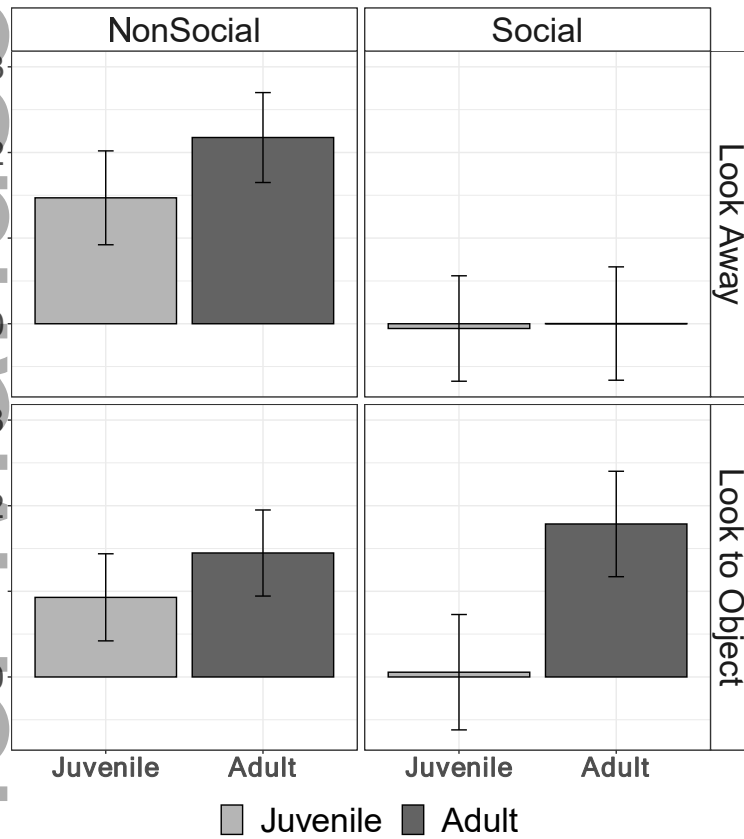


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Figure 2: Looking responses across habituation and test trials depending on cue and looking outcome. After an initial habituation trial (identical for all conditions), monkeys experienced either a *social cue* or *nonsocial cue*, and then observed 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.

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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.

