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3 **There is no Other Monkey in the Mirror for Spider Monkeys (*Ateles geoffroyi*)**

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23 Abstract

24 Mirror self-recognition (MSR), usually considered a marker of self-awareness, occurs in several
25 species and may reflect a capacity that has evolved in small incremental steps. In line with
26 research on human development and building on previous research adopting a gradualist
27 framework, we categorized the initial mirror responses of naïve spider monkeys (*Ateles*
28 *geoffroyi*) according to four levels. We compared social, exploratory, contingent and self-
29 exploratory responses to a mirror and faux mirror during three short trials. If spider monkeys
30 respond as most monkey species, we predicted they would perform at level 0, mainly showing
31 social behavior toward their mirror-image. However, because spider monkeys show
32 enhancement of certain cognitive skills comparable to those of great ape species, we predicted
33 that they would perform at level 1a (showing exploratory behavior) or 1b (showing contingent
34 behavior). GLMMs revealed that monkeys looked behind and visually inspected the mirror
35 significantly more in the mirror than the faux mirror condition. Although the monkeys engaged
36 in contingent body movements at the mirror, this trend was not significant. Strikingly, they
37 showed no social behaviors toward their mirror-image. We also measured self-scratching as an
38 indicator of anxiety and found no differences in frequencies of self-scratching between
39 conditions. Therefore, in contrast to most findings on other species, spider monkeys did not
40 treat their image as another monkey during their initial exposure to the mirror. In fact, they
41 reached at least level 1a within minutes of mirror exposure. These responses recommend spider
42 monkeys as good candidates for further explorations into monkey self-recognition.

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44 *Keywords:* spider monkeys, mirror self-recognition, self-awareness, gradualist framework

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47 There is no Other Monkey in the Mirror for Spider Monkeys (*Ateles geoffroyi*)

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49 Several studies have investigated whether species recognize themselves in the mirror
50 (reviewed in Anderson & Gallup, 2015; de Veer & van den Bos, 1999). The interest in mirror
51 self-recognition (MSR) largely stems from the fact that MSR is usually considered a marker of
52 self-awareness (e.g., Gallup, 1982; Anderson & Gallup, 2011), which implies ownership of a
53 self-concept and the ability to distinguish between the self and others, and may be highly
54 adaptive in group-living species (Bekoff & Sherman, 2003; Cenami Spada et al., 1995). To
55 date, clear evidence of MSR occurs in relatively few species, including great apes (e.g.,
56 Anderson, 1994; Anderson & Gallup, 1999; Gallup, 1970; Gallup et al., 2011), bottlenose
57 dolphins (*Tursiops truncatus*: Reiss & Marino, 2001), Asian elephants (*Elephas maximus*:
58 Plotnik et al., 2006), and Eurasian magpies (*Pica pica*: Prior et al., 2008), although often only in
59 a limited number of individuals of those species. Other species, in contrast, show no evidence of
60 MSR, failing to spontaneously recognize their image in a mirror (e.g., monkeys: see Anderson
61 & Gallup, 2015 for a review; parrots: van Buuren et al., 2018).

62 When exposed to a mirror, monkeys typically persist in perceiving their mirror-image as
63 an unfamiliar conspecific, even when given extended exposure and other facilitating cues such
64 as paired exposure (Gallup et al., 1980). In an experiment with brown capuchin monkeys
65 (*Sapajus apella*), de Waal et al., 2005) challenged the view that the monkeys were responding
66 as they would to unfamiliar conspecifics. A similar response occurs in cichlid fish
67 (*Astatotilapia burtoni*: Desjardins & Fernald, 2010).

68 A gradualist framework of the evolution of cognitive skills in small incremental steps
69 has been proposed to explain the variety of behaviors displayed by different taxa during mirror
70 exposure (e.g., de Waal, 2019; de Waal et al., 2005; de Waal & Ferrari, 2010; Murray, 2020).
71 This gradualist framework can better explain behaviors toward a mirror, such as aggressive

72 responses in some bird and monkey species, to quick habituation in dogs and cats, to its
73 instrumental use by some monkeys and parrots, and to self-exploration in great apes (see de
74 Waal, 2019, for a review; Murray, 2020). This framework also explains why some species show
75 some evidence of MSR after intensive training (e.g., Chang et al., 2015).

76 In line with research on human development (e.g., Rochat, 2001, 2003), in non-human
77 species, naïve individuals' responses to mirror exposure can be categorized according to
78 different levels. Here, we build on previous research (e.g., de Waal et al., 2005; Inoue-
79 Nakamura, 1997; Murray, 2020; Plotnik et al., 2006) to define the following four levels. Level 0
80 consists of individuals responding to their mirror image as they would to a conspecific, showing
81 aggressive and/or affiliative behavior. Level 1a consists of individuals exploring the mirror
82 without showing any aggressive and/or affiliative behavior. At level 1b, individuals start
83 connecting their image with their own body, performing unusual and repetitive behaviors in
84 front of the mirror, as if testing the contingencies between their body movements and those of
85 the image in the mirror. Finally, at level 2, individuals show self-exploration of body parts
86 which are not visible without a mirror. Individuals can also be tested for level 2 by marking
87 them with paint on the forehead and examining whether they touch the paint in their altered
88 image reflected in the mirror (e.g., Anderson & Gallup, 2011; Gallup, 1970).

89 We used the gradualist framework to evaluate spider monkeys' (*Ateles geoffroyi*) initial
90 responses to their image in a mirror. Spider monkeys are an interesting species to test for levels
91 higher than 0 because they show enhancement of certain cognitive skills comparable to great
92 ape species (e.g., Amici et al., 2008, 2010; Amici et al., 2018; Deaner et al., 2006), including
93 human-like holistic face processing (Taubert, 2010). Here, we assessed the response level of
94 seven spider monkeys to a brief exposure to a mirror and a faux mirror, by comparing their
95 social, exploratory, contingent and self-exploratory behaviors between the two conditions. We
96 kept the mirror exposure brief (5 minutes for each trial, for a total of three trials) as we focused

97 on spider monkeys' response level to the initial mirror exposure. If spider monkeys respond as
98 most monkey species, we predicted they would perform at level 0 by mainly showing social
99 behavior toward their image in the mirror. However, if their responses to mirror exposure are
100 related to the enhancement of cognitive skills, we predicted that they would perform at levels
101 1a, 1b or 2 by showing exploratory, contingent and self-exploratory behaviors, respectively.

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Method

104 Subjects and Study Site

105 We tested seven sexually mature spider monkeys (four females, three males) housed at
106 the Centenario Zoo in Merida, Mexico. They were wild born but were raised as pets before
107 being rescued and brought to the zoo. Spider monkeys were housed in well-established groups
108 in enclosures with outdoor and indoor areas. All subjects were used to being temporarily
109 isolated in the area of their enclosure where a familiar experimenter (FeA) individually tested
110 them. They had all previously participated in experimental tasks, but none of them had
111 previously been tested with a mirror, although we cannot exclude that they had been
112 inadvertently exposed to mirrors while they were kept as pets. Subjects participated in the trials
113 on a voluntary basis. Before and during testing, they were not deprived of food or water at any
114 time. The experimental protocols provided spider monkeys with a form of enrichment and were
115 approved by the Centenario Zoo and the University of Chester's School of Psychology Ethics
116 Committee.

117 Materials

118 A Clark's 600 mm x 450 mm safety mirror was used; this had a stainless steel polished
119 mirror quality surface on one side (used for the Mirror condition) and a non-reflecting brushed
120 steel surface on the reverse side, in which it was not possible to see reflections of forms, shapes

121 or colors (used for the Faux mirror condition). Febreze odor neutralizing spray was applied
122 between each trial to prevent olfactory cues.

123 **Procedure**

124 Subjects were tested alone in the familiar testing room. We used two rings to hang a
125 mirror in the testing room, so that subjects could peer behind it, but not move it. Subjects
126 received a small food reinforcement for entering the testing room and one at the end of the trial
127 before being released into the home enclosure. We administered two different conditions each
128 lasting 5 minutes. In the Mirror condition, the mirror was hanging in the testing room, with the
129 reflecting stainless polished surface facing the subject. In the Faux mirror condition, the mirror
130 was hung in the same position but with the non-reflecting brushed steel surface facing the
131 subject. All individuals received 3 trials for the Mirror condition and 3 for the Faux mirror
132 condition. The presentation of mirror type was counterbalanced, with some subjects starting
133 with the Mirror and some with the Faux mirror condition.

134 **Coding**

135 All trials were video-recorded, and later coded from the videos by two observers (i.e.,
136 CMS and LM). Cohen's weighted kappa tests were run to determine the level of agreement
137 between coders. Sampling one subject across two conditions, perfect agreement was found for
138 facial orientation ($k = 1.000$; $p < .0001$), and very high agreement was found for overall
139 behavioral classification ($k = 0.811$; $p < .0001$). We coded affiliative and agonistic behaviors,
140 indicative of level 0; exploratory behaviors, indicative of level 1a; contingent behaviors
141 (defined as visual alternation from the body part to the mirror, including slowly waving the
142 hand, moving slowly forward and backward, moving one leg slowly while standing on the other
143 foot), indicative of level 1b; and self-exploratory behaviors, indicative of level 2 (Table 1).
144 These behaviors were recorded when directed toward the mirror in the Mirror condition and
145 toward the non-reflecting side of the mirror in the Faux mirror condition. In addition, we coded

146 self-scratching as a potential indicator of anxiety (see Maestripietri et al., 1992 and Schino et al.,
147 1996 for evidence in other species; Table 1). All behaviors were coded as duration (i.e. total
148 seconds spent in the behavior during the 5-minute trial), except for look behind and self-
149 scratching, which were coded as frequency (i.e. total counts during the 5-minute trial).

150 (Insert Table 1 here)

151 **Statistical analyses**

152 Analyses were conducted using generalized linear mixed models (GLMMs: Baayen et
153 al., 2008) with the lme4 package in R (version 3.5.0; Bates, 2010). In each GLMM the
154 frequency or the time spent in one of the behavioral responses listed in Table 1 was the
155 dependent variable (following a Gaussian distribution, with normally distributed and
156 homogeneous residuals) and condition (Mirror or Faux mirror) was the predictor variable. In
157 each model, we included the subject's sex (i.e. male or female) and trial number (i.e. 1 to 3) as
158 control fixed factors, and the subject's identity as random factor. We compared full and null
159 models using a likelihood ratio test (Chatfield et al., 2002). In case of a significant difference
160 between full and null models, we conducted likelihood ratio tests to obtain the p values for each
161 test predictor via single-term deletion (Barr et al., 2013). No convergence or stability issues
162 were detected (except for some convergence issues in one model, see below).

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Results

166 *Level 0 – Social behaviors.* Monkeys showed no social behaviors (i.e., agonistic
167 behavior, affiliative behavior, fear) toward their image in the mirror, in any trial. No model was
168 therefore run.

169

170 *Level 1a – Exploration.* Six of the seven monkeys looked behind the mirror with a mean
171 latency of 49 seconds in trial 1 (videos 1-3 in SM). The comparison between the full and null
172 model for looking behind the mirror was significant (GLMM: $\chi^2 = 6.30$, $df = 1$, $p = .012$);
173 monkeys looked behind the mirror more often than the faux mirror (Table 2; Figure 1). The
174 comparison between the full and null model for physical inspection of the mirror was not
175 significant (GLMM: $\chi^2 = 0.58$, $df = 1$, $p = .445$; see Table 2), suggesting no differences in the
176 physical inspection of either the mirror or the faux mirror between the two conditions. All seven
177 monkeys engaged in visual inspection of the mirror, with a mean latency of 34 seconds in trial 1
178 (videos 1-4 in SM). For visual inspection of the mirror, the comparison between the full and
179 null model was significant (GLMM: $\chi^2 = 4.21$, $df = 1$, $p = .040$); monkeys visually inspected the
180 mirror more often than the faux mirror (Table 2; Figure 1). In all instances of look behind and
181 visual inspection of the mirror, the monkeys did not do anything else than move around their
182 enclosure prior to approaching the mirror.

183

184 (Insert Table 2 here)

185 (Insert Figure 1)

186 *Level 1b – Contingent behaviors.* Four of the seven monkeys showed contingent body
187 movements in front of the mirror with a mean latency of 58 seconds in trial 1 (videos 1, 3 and 4
188 in SM). The comparison between the full and null model did not reach significance (GLMM: χ^2
189 = 3.33, $df = 1$, $p = .068$) but the tendency was for the subject to have a higher probability of
190 performing contingent body movements in the Mirror condition than in the Faux mirror
191 condition (Table 2; Figure 1, video 2 in SM). Monkeys showed no contingent facial movements
192 in any trial, so no model was run for this variable.

193

219 behavior. Our result on social behaviors contrasts with research on other species, which failed to
220 immediately differentiate their mirror image from that of a conspecific, and often showed social
221 behaviors even after several hours of mirror exposure. Social behaviors during initial mirror
222 exposure occur in other New World monkey species (e.g., cotton-top tamarins, *Saguinus*
223 *oedipus*, and squirrel monkeys, *Saimiri sciureus*: Inoue-Nakamura, 1997; brown capuchin
224 monkeys, *Sapajus apella*: Anderson & Roeder, 1989; de Waal et al, 2005), by several species of
225 macaques (e.g., rhesus macaques, *Macaca mulatta*: Inoue-Nakamura, 1997; Rajala et al., 2010;
226 Suarez & Gallup, 1986; long-tailed macaques, *M. fascicularis*: Gallup, 1977; stump-tailed
227 macaques, *M. arctoides*; Anderson, 1983; bonnet macaques, *Macaca radiata*: Inoue-Nakamura,
228 1997; but see Japanese macaques, *M. fuscata*: Inoue-Nakamura, 1997) and by gibbons
229 (*Hylobates*, *Symphalangus* and *Nomascus spp.*; Inoue-Nakamura, 1997; Suddendorf & Collier-
230 Baker, 2009; Ujhely et al, 2000). Remarkably, all four great apes exhibit some social behavior
231 during initial mirror exposure (e.g., Inoue-Nakamura, 1997 for chimpanzees, *Pan troglodytes*,
232 gorillas, *Gorilla gorilla*, and orangutans, *Pongo pygmaeus*; Walraven et al, 1995 for bonobos,
233 *Pan paniscus*). Gallup (1970), for example, reported that chimpanzees repeatedly engaged in
234 social behaviors towards their mirror image, with a substantial reduction only after around 20
235 hours of mirror exposure.

236 Very few studies to date have shown a lack of social responses during initial mirror
237 exposure: bottlenose dolphins (Reiss & Marino, 2001), Asian elephants (Plotnik et al., 2006),
238 and Western gorillas (Posada & Colell, 2007). Therefore, the performance of spider monkeys in
239 our study is remarkable. Although our study only provides a preliminary understanding of
240 spider monkeys' reaction to mirrors, it is noteworthy given that spider monkeys already show
241 cognitive skills comparable to those of great apes (e.g., Amici et al., 2008, 2010; Amici et al.,
242 2018; Deaner et al., 2006).

243 Secondly, spider monkeys looked behind and visually inspected the mirror more often
244 than they did the faux mirror. Our results suggest that spider monkeys reached level 1a in trial
245 1, after less than a minute of mirror exposure. Although four of the seven monkeys engaged in
246 some contingent body movements while facing the mirror within a minute of mirror exposure,
247 we found no significant difference between the mirror and the faux mirror conditions. This is
248 something requiring further investigation, considering that contingent behaviors have been
249 taken as evidence of level 1b (e.g., de Waal et al., 2005; Inoue-Nakamura, 1997; Plotnik et al.,
250 2006). The spider monkeys showed no evidence of self-exploration (i.e. level 2), which is
251 unsurprising given the reduced exposure to the mirror. Importantly, the different responses
252 shown by spider monkeys in the mirror condition compared to the faux mirror condition cannot
253 be explained by differences in individuals' anxiety. Indeed, subjects did not differ in the self-
254 scratching rate between conditions.

255 Our study provides a first assessment of spider monkeys' response to mirrors, which
256 revealed that spider monkeys reach at least level 1a after only minutes of mirror exposure.
257 Future studies should investigate spider monkeys' response to mirrors by focusing on the
258 following aspects. Firstly, our findings of no occurrence of social behavior should be replicated
259 with subjects that were not previous pets. Although in the Yucatan peninsula spider monkey
260 pets are usually kept outdoors, where mirrors are typically absent, some experience with mirrors
261 could have influenced our study subjects' performance. Secondly, future studies should include
262 observation of spider monkeys' reactions to other monkeys to directly compare mirror
263 responses with how monkeys typically interact with one another. Thirdly, subjects should be
264 tested for a longer time, and with alternative stimuli such as video proxies of the mirror, to
265 evaluate whether spider monkeys reach further levels of response to mirror exposure. Should
266 spider monkeys perform like dolphins, elephants and great apes, there will be further support to

267 the view that spider monkeys show an enhancement of certain cognitive skills. Such discovery
268 will also provide renewed impetus for a revised perspective on MSR.

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Table 1

Behavioral responses (adapted from Povinelli et al., 1993) according to Self-Recognition (SR) continuum framework (Murray, 2020)

Level	Behavioral responses	Description
L0 - No self-recognition	Agonistic behavior	Subject shows aggressive behaviors toward the mirror (e.g., threat faces, charging)
	Social behaviors	Fear Subject shows grimaces, escape behavior and/or squeals Affiliative behavior Subject shows affiliative behaviors toward the mirror (e.g., face greeting, tee-tee vocalizations, play invitations, sexual presentations)
L1a – Differentiated responses to mirror	Look behind	Subject lifts the mirror to inspect its back or peers over its edge to view its reverse side
	Exploration	Mirror physical inspection Subject touches the mirror with hands, feet, mouth, nose or tail Mirror visual inspection Subject explores the mirror by looking at it without touching it
L1b - Differentiated responses to video (or mirror) including contingency-checking	Contingent behaviors	Contingent body movements Subject makes purposeful or repetitious body movements, while facing the mirror (e.g., the subject's face is oriented toward its body, then to the mirror and back; hands or arms are slowly waved in front of the mirror; side to side or backward/forward body movements in front of the mirror) Contingent facial movements Subject makes unusual face movements, while facing the mirror
	L2 – Self-exploratory behavior	Body self-exploration
Self-exploration		Face self-exploration Subject uses fingers, hand or tail to examine its face or mouth, while facing the mirror
Anxiety indicator	Self-scratching	Subject repeatedly rubs its body with the fingers

Note. All behaviors were coded as duration (in seconds), except for look behind and self-scratching, which were coded as counts. For self-scratching, a new event was scored after a pause of 5 seconds.

Table 2

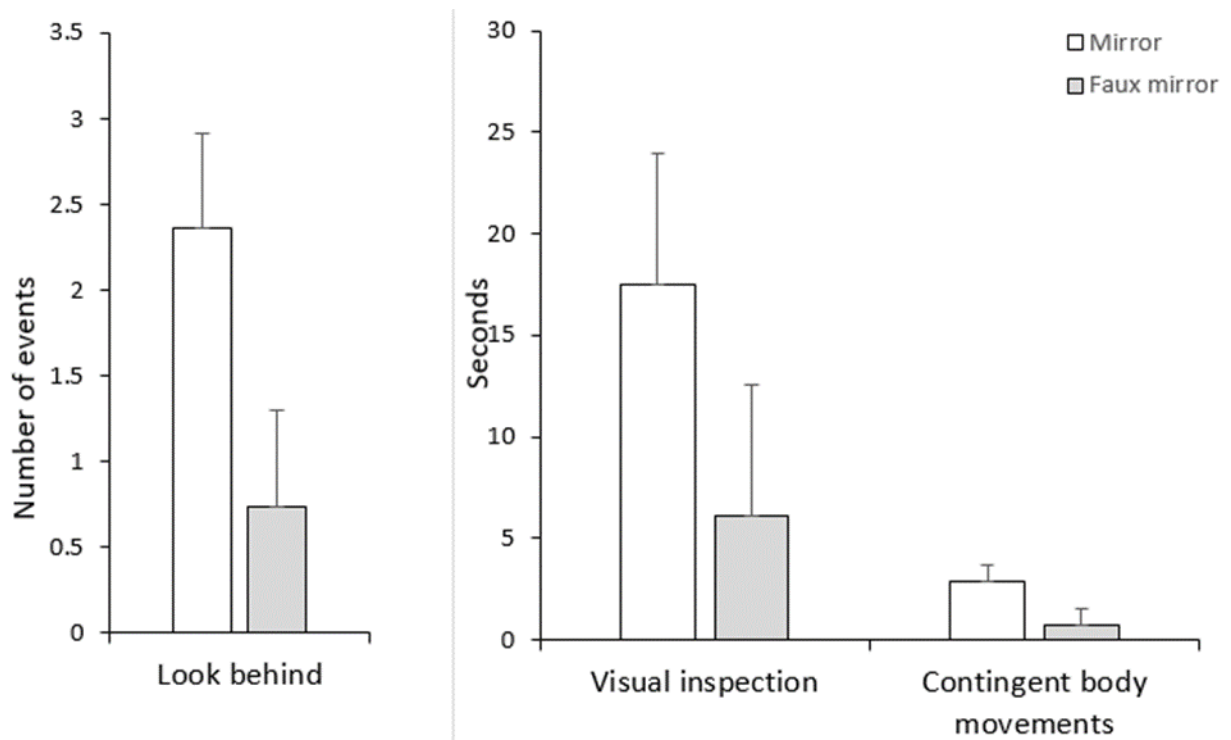
Results of GLMM models, including estimates, standard errors (SE), confidence intervals (CIs), likelihood ratio tests (LRT), degrees of freedom (df) and P values

	Estimate	SE	2.5% CI	97.5% CI	LRT	df	P
<u>Looking behind</u>							
Intercept	2.85	1.10	0.81	4.89	-	-	-
Condition	1.62	0.63	0.38	2.86	6.30	1	0.001
Trial number	-1.14	0.39	-1.90	-0.38	8.15	1	0.002
Sex	0.35	1.08	-1.71	2.40	0.14	1	0.704
<u>Physically inspecting</u>							
Intercept	8.40	3.88	1.03	15.77	-	-	-
Condition	-1.90	2.59	-6.89	3.08	0.58	1	0.445
Trial number	-2.54	1.58	-5.59	0.51	2.69	1	0.101
Sex	3.13	2.80	-1.91	8.16	1.50	1	0.220
<u>Visually inspecting</u>							
Intercept	16.07	10.52	-3.42	35.55	-	-	-
Condition	11.38	5.54	0.53	22.23	4.21	1	0.040
Trial number	-7.61	3.40	-14.25	-0.96	4.96	1	0.026
Sex	10.57	11.51	-11.44	32.58	1.09	1	0.296
<u>Contingent body movements</u>							
Intercept	3.99	1.79	0.58	7.40	-	-	-
Condition	2.14	1.21	-0.16	4.45	3.33	1	0.068
Trial number	-2.07	0.74	-3.48	-0.66	7.86	1	0.005
Sex	1.69	1.22	-0.64	4.03	2.07	1	0.150
<u>Self-scratching</u>							
Intercept	2.29	0.94	0.53	4.04	-	-	-
Condition	0.19	0.58	-0.94	1.32	0.12	1	0.734
Trial number	-0.86	0.35	-1.55	-0.16	5.73	1	0.017
Sex	0.56	0.83	-1.04	2.15	0.60	1	0.440

Note. Significant effects of test predictors are in bold.

Figure 1

Estimated marginal means (+ SE) of the probability of looking behind the mirror/faux mirror, visually inspecting the mirror/faux mirror and performing contingent body movements in the Mirror condition and in the Faux mirror condition



Supplementary Materials

Video 1

Spider monkey engaged in Visual inspection, Contingent body movement, Look behind and Self-scratching in front of the mirror

Video 2

Spider monkey engaged in Visual inspection, Look behind and Physical inspection of the mirror

Video 3

Spider monkey engaged in Visual inspection, Look behind, Contingent body movement and Physical inspection of the mirror

Video 4

Spider monkey engaged in Visual inspection and Contingent body movement in front of the mirror