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1 Face processing limitation to own species in primates, a response to social needs?

2

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7 Face recognition in primates, Dufour et al.

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23 Most primates live in social groups which survival and stability depends on individuals' abilities
24 to create strong social relationships with other group members. The existence of those groups
25 requires to identify individuals and to assign to each of them a social status. Individual
26 recognition can be achieved through vocalizations but also through faces. In humans, an
27 efficient system for the processing of own species faces exists. This specialization is achieved
28 through experience with faces of conspecifics during development and leads to the loss of
29 ability to process faces from other primate species. We hypothesize that a similar mechanism
30 exists in social primates. We investigated face processing in one Old World species (genus
31 *Macaca*) and in one New World species (genus *Cebus*). Our results show the same advantage
32 for own species face recognition for all tested subjects. This work suggests in all species tested
33 the existence of a common trait inherited from the primate ancestor: an efficient system to
34 identify individual faces of own species only.

35

36 Keywords: Face recognition, brown capuchin monkeys, Tonkean macaques, evolution

37

37 There are several lines of evidence that the face processing system presents similarities between
38 different species. First, faces represent a highly attractive stimulus for infant primates, including
39 humans (*Homo sapiens*) (Goren et al. 1975), pigtailed macaques (*Macaca nemestrina*) (Lutz et
40 al. 1998), gibbons (*Hylobates agilis*) (Myowa-Yamakoshi & Tomonaga 2001) and chimpanzees
41 (*Pan troglodytes*) (Kuwahata et al. 2004). Three-week-old lambs (*Ovis ovis*) spend more time
42 sniffing a picture of sheep than a picture displaying other stimuli (Porter & Bouissou 1999).
43 Second, in most primate species, faces are a way to communicate emotions via the production
44 of mimics (van Hoof 1967; Parr 2003; Niedenthal et al. 2000). Third, neurons responding
45 specifically to faces compared to other stimuli have been found in non human primates (Perrett
46 et al. 1992) and in sheeps (Kendrick et al. 2001). In human a face specific electrophysiological
47 response, named the N170, is elicited by faces (Bentin et al. 1996; de Haan et al. 2002). Such
48 similarities may reflect a common origin selected by evolution (Campbell et al. 1997).
49 In the present study we investigate if the advantage of face processing to own species found in
50 humans (Pascalis et al. 2002; Dufour et al. 2004) and in rhesus macaques (*Macaca mulatta*)
51 (Pascalis & Bachevalier 1998) can be found in 2 other non human primate species, Tonkean
52 macaques (*Macaca tonkeana*) and brown capuchin monkeys (*Cebus apella*), which will give
53 convincing evidence to a common origin of the face recognition system.

54 We shall first review the similarities between the face processing system in human and
55 non human primates. Even if the morphological variability between human faces is limited,
56 human adults are very efficient at recognizing faces; they are able to discriminate hundreds of
57 them (Bahrick et al. 1975). It has been suggested that we differentiated individuals' faces on the
58 basis of relational information, such as the particular distance between the eyes, or between lips
59 and chin (Leder & Bruce 2000). The ability to process these parameters is called *configural*
60 processing and contrasts with feature processing (Diamond & Carey 1986; Maurer et al. 2002).
61 Yin (1969) has shown that faces are recognized more accurately and faster when presented in
62 their canonical orientation than when presented upside-down. A widely accepted claim is that

63 the cause of the inversion effect is a disruption of configural processing leading to the use of a
64 less efficient feature processing (Diamond & Carey 1986; Leder & Bruce 2000; Maurer et al.
65 2002). Valentine's (1991) model suggests that faces are encoded as individual points within a
66 multidimensional face space defined by a set of dimensions (gender, eye color, etc.). Valentine
67 proposes a norm-based coding model, whereby faces are encoded as vectors according to their
68 deviation from the central tendency, or prototypical average of the face space. It can explain the
69 other-race effect that is that adults find it easier to differentiate faces from their own-ethnic
70 group (Meissner & Brigham 2001). The human face processing system doesn't however extend
71 toward faces of other primate species that share the same face configuration (Dufour et al. 2004;
72 Pascalis et al. 2002).

73 Conspecifics' face identification is present in non human primates and can be studied
74 using pictures (Pascalis et al. 1999, for a review). For example, Dasser (1987) showed that
75 longtailed macaques could associate the picture of a member of their group to the real
76 individual. Individual's faces discrimination based on pictures has been demonstrated in
77 chimpanzees (Parr et al. 1998), Japanese macaques (*Macaca fuscata*) (Tomonaga 1994) and
78 rhesus macaques (Wright & Roberts 1996; Pascalis & Bachevalier 1998; Parr et al. 1999)
79 among other species. It is important to highlight that those abilities are not restricted to primates
80 but can be observed in other species, such as sheep. Sheeps can categorise their species based on
81 faces (Kendrick et al. 1995). They can also discriminate sheeps of their own breed from sheeps
82 of other breed, and between two individuals from their own breed as measured with a two-way
83 discrimination task (Kendrick et al. 1996).

84 Similarities in the face processing system include also the inversion effect. Face
85 recognition is sensitive to inversion in sheep (Kendrick et al. 1996) but its presence is still
86 debated for non human primates. In chimpanzees, Tomonaga et al. (1993) did not observe an
87 inversion effect for chimpanzees or humans familiar faces but they tested only one subject with
88 a limited number of stimuli. More recently, Parr et al. (1998) demonstrated an inversion effect

89 in 5 chimpanzees, for human and chimpanzee faces but not for capuchin faces or cars. In
90 longtailed macaques, Bruce (1982) did not observe an effect of inversion using a concurrent
91 discrimination task. Overman and Doty (1982), using a matching-to-sample task, found an
92 inversion effect in pigtailed macaques for both human and macaque faces. An inversion effect
93 was also demonstrated in a squirrel monkey (*Saimiri sciureus*) by Phelps and Roberts (1994) for
94 human faces (but not for monkey faces). The discrepancy observed in the non human primate
95 literature might be due to several factors such as the experimental paradigms that are different.
96 However, since face recognition in sheep is sensitive to inversion, the possibility of the
97 existence of inversion effect in monkeys cannot be rejected.

98 Nelson (2001) has suggested that the systems underlying human face processing may be
99 sculpted by experience with different kinds of faces present in the visual environment. The face
100 processing system is indeed developing until teenage hood (Carey & Diamond 1994; Campbell
101 et al. 1999). The early system is able to cope with different type of faces, for example, Pascalis
102 et al. (2002) showed that 6-month-old humans discriminated between both human and monkey
103 faces, but that 9-month-olds and adults discriminated only between human faces. Many
104 researchers attribute the other-race and other-species effects to the relatively common
105 experience of having greater exposure to faces of ones own-race compared to other races and
106 greater experience with faces within ones own species compared to other species (Valentine
107 1991; Nelson 2003). Thus we are best at recognizing faces similar to those we see most often in
108 our environment. However, it is important to differentiate between *other-race faces*, which
109 belong to the same face category as own-race faces (i.e. human faces), and *other-species faces*,
110 which belong to a separate face category (i.e. non human primate). While the face processing
111 system remains flexible for the category of faces to which we are most exposed, humans, this
112 plasticity may not extend for other face categories. Human adults process human faces at an
113 individual level whereas they process other species (monkey, sheep, etc.) at a category level.
114 Experience with other species during infancy seems to be important for the development of the
115 face processing system. In sheep, Kendrick et al. (1998) showed that male sheep reared by goats

116 (*Capra aegagrus hircus*) and male goats reared by sheep preferred to socialize with females
117 from their maternal species compared with their genetic species. In non human primates, visual
118 preference for maternal species has also been shown for chimpanzees reared by humans
119 (Tanaka 2003) and for Japanese monkeys reared by rhesus macaques (Fujita 1990, albeit not
120 true for rhesus macaques). Pascalis et al. (2005) demonstrate that exposure to Barbary macaques
121 faces (*Macaca Sylvanus*) - between 6 and 9 months of age- facilitates the discrimination of
122 monkey faces, in human infants, an ability that is otherwise lost around 9 months of age. The
123 adults' human limitation to process own-species faces has been observed in non human primates
124 (Pascalis & Bachevalier 1998) and sheep (Kendrick et al. 1996). However, Pascalis and
125 Bachevalier (1998) did not test for the abilities of rhesus macaques to recognize other non
126 human primate species that might have been morphologically closer than human faces. There is
127 indeed evidence that non human primates can discriminate faces of other species. Parr et al.
128 (1998) showed that chimpanzees could learn to discriminate between faces of humans, of their
129 own species, of brown capuchins and between pictures of cars in a sequential matching-to-
130 sample task. Rhesus macaques tested with the same paradigm (Parr et al. 1999) revealed similar
131 ability albeit following a longer training phase. Wright and Roberts (1996) using a two-
132 alternative forced choice task, showed that rhesus macaques could discriminate between human
133 and various species of monkey faces. Other studies confirmed, however, the limitation to
134 process own-species faces. Humphrey (1974) with a habituation dishabituation task showed that
135 rhesus monkeys discriminated between two conspecifics but not between two individuals of
136 another species. Kim et al. (1999), using a visual paired comparison task showed that young
137 pigtailed macaques discriminated faces of their own species but not humans or longtailed
138 macaques faces. From this review, the existence of a limitation to own species in other non
139 human primates remains to be explored. It is indeed not clear whether the face system could
140 extend to the processing of phylogenetically close species faces, process that could be based on
141 morphological proximity of those faces.

142

143 Our aim was to study inter-individual discrimination of faces of different species in a
144 wider range of primates with the same technique as the one used by Pascalis and Bachevalier
145 (1998). We investigated face recognition in humans, brown capuchins and Tonkean. Each
146 species tested had none or limited experience with other primate species. In order to test the
147 common origin of the face system, we tested the face processing ability of one macaque species
148 that radiated a few million years before the anthropoid branch, but also of brown capuchin
149 monkeys who diverged earlier than macaques from the ancestral lineage (Fig. 1). Moreover, we
150 explored if the recognition ability extended to phylogenetically close species *i.e.* same-genus
151 species, or was restricted to the recognition of their own species. Therefore, the subjects were
152 tested with faces of more or less close species. We used the visual paired comparison (VPC)
153 task which indexes the relative interest in a pair of visual stimuli consisting of one novel item
154 and one familiar item viewed during a prior familiarization period (Pascalis & de Haan 2003).
155 Recognition is inferred from the participant's tendency to fixate more towards one stimulus than
156 the other; usually the novel stimulus. This task can be used with both human and non human
157 primates.

158 The VPC task is rather an unusual task to study face recognition in non human primates.
159 It is mainly used to study cognition in both human and non human primate infants but has been
160 recently used successfully to study the neural substrate of recognition memory in monkeys. The
161 VPC has been found to be more sensitive to detect memory deficits after cortical lesions than
162 classic matching tasks (Pascalis & Bachevalier, 1999; Zola et al., 2000; Nemanic et al., 2004).

163

164

165

MATERIAL AND METHODS

166

167 Subjects

168

169 Five men and four women aged from 23 to 55 years (mean 32 years) were tested at the
170 University of Strasbourg. None of the participants had previous experience with monkeys. Non
171 human subjects were five Tonkean macaques aged from 3 to 11 years old (three females and
172 two males) and five brown capuchin monkeys aged from 3 to 29 years (three females and two
173 males). Subject were all mother reared in social groups. One Tonkean macaque (male) had been
174 isolated for social reasons in an individual cage 1 year before the beginning of the experiment.
175 The other Tonkean macaques were socially housed in an indoor cage of 20-meter square
176 composed of two compartments, connected to a tunnel leading to the testing room. Capuchin
177 monkeys belonged to a social group of 18-22 individuals living in an indoor-outdoor enclosure
178 composed of 78 meter square in total (33 meter square inside, 45 meter square outside). Cages
179 and enclosure of all subjects were furnished with wooden perches and plastic elements.

180 All subjects had an ad libitum access to commercial monkey diet and water. In addition, they
181 received fresh fruit supply once a week. They were never deprived in food or water.

182

183 Stimuli

184

185 Humans performed 2 trials per category of stimuli. Each trial consisted in a
186 familiarization period with a face followed by a recognition test during which two faces, one
187 new and one being the familiar seen previously were presented. Participants performed 2 trials
188 with human faces, 2 trials with rhesus macaques faces and 2 trials with Tonkean macaques faces
189 Human were tested in order to replicate previous results that showed species specificity in
190 humans (Pascalis & Bachevalier, 1998; Pascalis et al., 2002) with a different set of stimuli.

191 Non-human primates were tested with four categories of faces, with 10 trials per category.
192 Tonkean macaques were tested with faces of their own species, of stumptailed macaques
193 (*Macaca arctoides*) of rhesus macaques and of humans. Brown capuchin monkeys were tested
194 with faces of their own species, of white-faced capuchins (*Cebus capucinus*) that belong to the
195 same genus, of longtailed macaques and of humans. Stimuli were black and white pictures of
196 unfamiliar individuals. For human as well as for non human primates, contrast and brightness
197 were visually adjusted so as to make pictures appear as similar as possible. It was achieved by
198 controlling the level of contrast and brightness of each paired stimuli using the software
199 *AdobePhotoshop*. Macaques' faces were extracted from Dr B. Thierry private's collection.
200 Capuchin pictures were taken in various French zoological parks, with semi-free individuals
201 that could be seen from a close distance and without mesh. Faces were selected for their neutral
202 expression. They were paired with individual of the same sex. Only frontal view or faces
203 deviating slightly from frontal view were selected. Faces were consequently paired so as to
204 match in their orientation. Figure 2 shows an illustration of the stimuli used.

205

206 Procedure

207 *Testing*

208 The procedure used for humans is comparable as the one described by Pascalis et al.
209 (2002). Participants were asked to relax and passively view the images that would appear on the
210 screen approximately 60 cm away in front of them. A black and white CCD camera filmed the
211 participant's eye movements for further analysis. Time was recorded and displayed on the
212 control monitor using an Horita (TG-50) at 25 frames per second. The experimenters
213 predetermined a series of images for participant. Each trial consisted of a familiarization period
214 during which a single image was displayed for 3 s from the first time of looking, followed by a
215 blank interval of 3 s, followed by the recognition test that consisted in the presentation of two
216 images, one novel and one familiar, for 3 s. The left-right position of the novel and familiar

217 stimuli was counterbalanced across the testing. The testing of human participants was done over
218 two days. Non-human primates were first isolated from the group and trained to look at the
219 projection screen distant to the cage from one meter. Monkeys were given orange juice each
220 time they looked toward the screen to maintain their attention. Sessions ended as soon as the
221 level of interest of the subject for the experiment declined. One session lasted generally for 4 to
222 12 trials. Subjects were tested daily before returning into their social group. Training and testing
223 required about 3 months per individual. The Tonkean macaques came from different groups and
224 their testing was done between June 1999 and January 2001. Capuchin monkeys testing began
225 in June 2002 and lasted until March 2003. For non human primates, the familiarization period
226 ended when each stimulus was presented for a total cumulated time of 3 s. The interval lasted 3
227 s. The recognition test was 3 s of cumulated time. It insured that each participant (whatever the
228 species) watched the stimuli for a similar amount of time. The experimenter estimated the total
229 cumulated time by observing the subjects' behaviour through the monitor. The familiarization
230 time was later controlled picture by picture using the software *the observer*. Using the same
231 software, participant's behaviour during the preference test was then analyzed by measuring
232 time spent looking on the left or on the right stimulus. This was assessed by tracking on videos
233 the corneal reflection of the slide (Fig. 3). Trials were scored by an experimenter, who was not
234 aware of the position of the familiar and novel stimuli.

235

236 Data analysis

237 Statistical analyses were realized on real looking time in humans. In non human
238 primates, the amount of time spent exploring the pictures varied widely between the species, so
239 the data were normalized. For the three species tested, analyses of variance with repeated
240 measures were conducted on the amount of time spent looking at the stimuli considering the
241 following factors: subject, direction of gaze (towards the new stimulus and the familiar) and

242 category of stimuli. Data were further analyzed per category of stimuli, with one-tailed paired t-
243 tests.

244

245

246

RESULTS

247 For humans, an analysis of variance of the time spent looking at each face (the new and
248 the familiar) reveals an effect of the direction of the gaze ($F_{1,8} = 6.03$; $P = 0.04$), participants
249 spent more time looking at the novel pictures. Detailed analysis for each category of face shows
250 that this novelty preference is statistically significant only for human faces as revealed by one
251 tailed paired t-test ($T = 2.34$, $df = 8$, $P = 0.03$). There is no evidence of preference for novel or
252 familiar stimuli for faces of another primate species (one tailed paired t-tests for rhesus
253 macaque, $T = 1.31$, $df = 8$, $P = 0.11$; for Tonkean macaques, one tailed paired $T = 0.64$, $df = 8$,
254 $P = 0.27$) (Fig. 4). This result replicates previous results showing that recognition of faces, as
255 measured with a VPC task, is limited to own species in human adults (Pascalis & Bachevalier
256 1998; Pascalis et al. 2002).

257 Tonkean macaques were shown paired faces of their own species, of rhesus macaques,
258 of stumptailed macaques and of humans. Results of the analysis of variance reveal an effect of
259 the species ($F_{3,12} = 5.88$; $P = 0.0008$). Subjects looked longer at Tonkean macaques' faces
260 compared to faces of another species (contrast post-hoc test: Tonkean macaques versus others: P
261 $= 0.0183$). A one tailed paired t-test shows that subjects looked longer at the new stimulus when
262 tested with faces of their own species ($T = 1.73$, $df = 49$, $P = 0.04$). This novelty preference is
263 not found for faces of stumptailed macaques (one tailed paired $T = 1.21$, $df = 49$, $P = 0.12$),
264 rhesus macaques (one tailed paired $T = 0.65$, $df = 49$, $P = 0.26$), or humans (one tailed paired $T =$
265 0.99 , $df = 49$, $P = 0.16$) (Fig. 4). As humans, Tonkean macaques present visual recognition only

266 for their own species. It extends the results obtained with rhesus macaques by Pascalis and
267 Bachevalier (1998).

268 Concerning brown capuchin monkeys, the analysis of variance reveals that subjects
269 looked longer when faces of their own species were shown, compared to other species (main
270 effect: species, $F_{3,12} = 5.21$, $P = 0.002$; contrast post hoc test, brown capuchin monkeys versus
271 the others: $P = 0.0196$). Novelty preference was found for brown capuchins' faces (one tailed
272 paired t-test: $T = 2.27$, $df = 49$, $P = 0.01$) (Fig. 4), but not for faces of white-faced capuchins
273 (one tailed paired $T = 0.24$, $df = 49$, $P = 0.4$), longtailed macaques (one tailed paired $T = 0.71$,
274 $df = 49$, $P = 0.24$) or humans (one tailed paired $T = 0.091$, $df = 49$, $P = 0.46$). A species-specific
275 limitation in the recognition of faces is also observed in brown capuchin monkeys.

276

277

DISCUSSION

278

279 In both humans and non human primates tested in this study, we found the same limitation of
280 recognition to own species faces. No evidence of recognition was found even for
281 phylogenetically close species. These results support the hypothesis of a species-specific face
282 recognition system in adults' primates. We observed that Tonkean macaques and brown
283 capuchin monkeys looked longer at the pictures that presented their own species. This result is
284 consistent with Fujita's study (1987) that showed that different species of macaques pressed a
285 lever longer to see pictures of their own species compared with pictures of other macaque
286 species.

287 Our results are however contradictory to other results from the literature that found that
288 non human primates could process faces of other species. For example, Parr et al. (2000)
289 showed that human-reared chimpanzees are able to discriminate between human faces as
290 assessed in a forced choice task. The difference may reflect a methodology issue. The visual

291 paired comparison task is a way to assess spontaneous recognition as it doesn't involve any
292 training or reward. By contrast, the matching to sample paradigm requires extensive training
293 and monkeys with poor recognition performance at the beginning could purposely used a
294 special behavioral strategy to succeed, that is they may process the faces of other-species in a
295 very different way than their own species faces (Ridley & Baker 1991; Pascalis & Bachevalier
296 1999). The same pattern of results is observed in humans who do not present evidence of
297 discrimination of other species faces with the VPC but can do it in a forced choice task (Dufour
298 et al. 2004). However when the stimulus' presentation time is short, humans succeed only at
299 recognizing human faces in a forced choice task. Our results show that the face recognition
300 system does not automatically process faces of another species.

301 There is a second explanation for the discrepancy observed between the results of this
302 study and of Parr et al. (2000) study. In humans, early exposure influences face processing
303 abilities (Pascalis et al. 2005); similar mechanisms could exist in non human primates. Our non
304 human primate population was naturally reared by their mother in their own species social
305 group and encountered only sometimes humans in their environment (keepers, primatologists).
306 Such limited experience was insufficient to allow our non human primates to discriminate
307 between human faces whereas extensive experience may have sculpted the chimpanzees face
308 processing toward human faces. It would be consistent with Nelson's hypothesis (Nelson 2001)
309 of an experience dependent face recognition system for non human primates.

310 The ability to discriminate at first sight between unknown individuals of its own species may
311 represent a strong advantage when living in social groups, whereas categorizing individuals as
312 not being from its own species is efficient enough. From an evolutionary point of view, such a
313 system may be more economical than a system allowing discrimination between any faces of
314 any primate species and could have been privileged by natural selection. Inability to
315 spontaneously discriminate between individuals of another primate species could also prevent
316 hybridization. The primates face recognition system demonstrates complex abilities and a high

317 degree of specialization. It may have been an important tool toward the development of most
318 primate societies that are based on strong social relationships (Thierry 1994).

319

320 The face discrimination limitation in primates may provide evidence that the common
321 ancestor to actual living social primates needed such a specialized system to develop a social
322 organization. In primates, the development of three-dimensional vision, with two eyes frontally
323 oriented and the shortening of the “nose” (Simons 1963) occurred around 45 millions of years
324 ago. In primate history, macaques separated 15 millions of years ago and capuchins lineage
325 diverged between 45 and 28 millions of years ago (Kay et al. 2002). As we showed, this latter
326 New World species has the same limitation in its face recognition system than other primates.
327 Thus, we can assume that the selection of such a face recognition system will be anterior to the
328 radiation of the capuchin ancestor from the primate order. The system would have kept
329 comparable abilities throughout evolution. One way to confirm this hypothesis would be to
330 study lemurs’ face recognition ability. Lemurs separated earlier than capuchins inside the
331 primate order, their communication relies more on olfactory than on visual cues (Gosset et al.
332 2003) and they do not show the “face like” pattern as simians do.

333

334

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338

339

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474 Figure 1: Main dates of radiation inside the primate order.

475 Figure 2: Illustration of the stimuli shown to participants. a: *Homo sapiens*, b: *Macaca*

476 *fascicularis*, c: *Macaca Tonkeana*, d: *Macaca mulatta*, e: *Macaca arctoides*, f: *Cebus apella*, g:

477 *Cebus capucinus*.

478 Figure 3: Illustration of gaze direction toward right (a) and left (b) stimuli in one capuchin. The

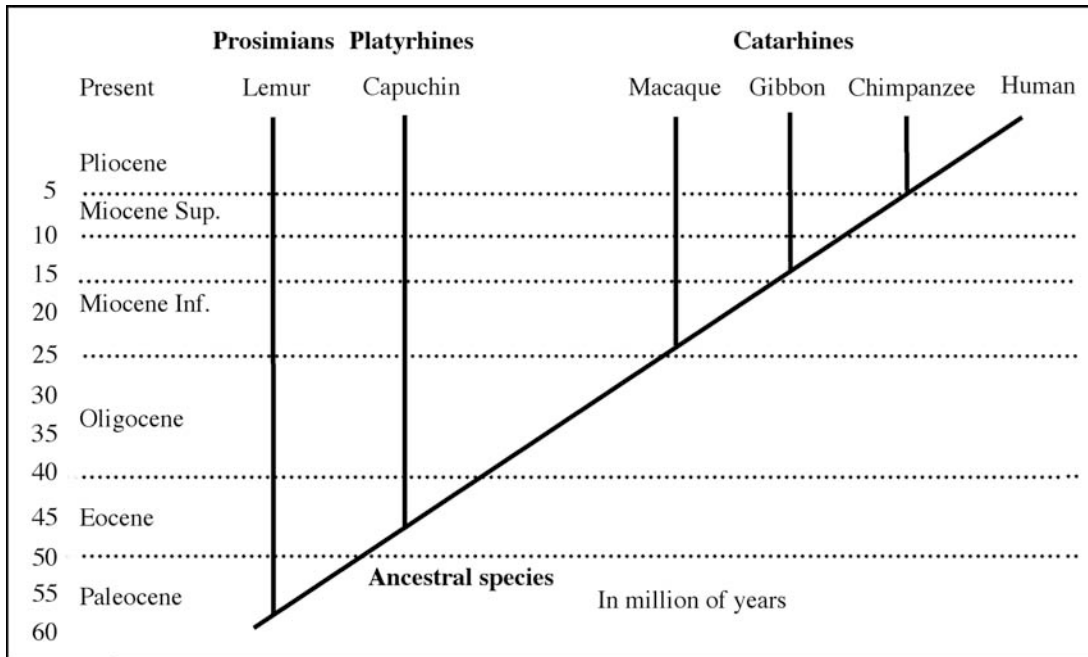
479 corneal reflection of the slide on the left or on the right part of the cornea indicates the direction

480 of looking.

481 Figure 4: Time spent looking toward the new and familiar stimulus for each species

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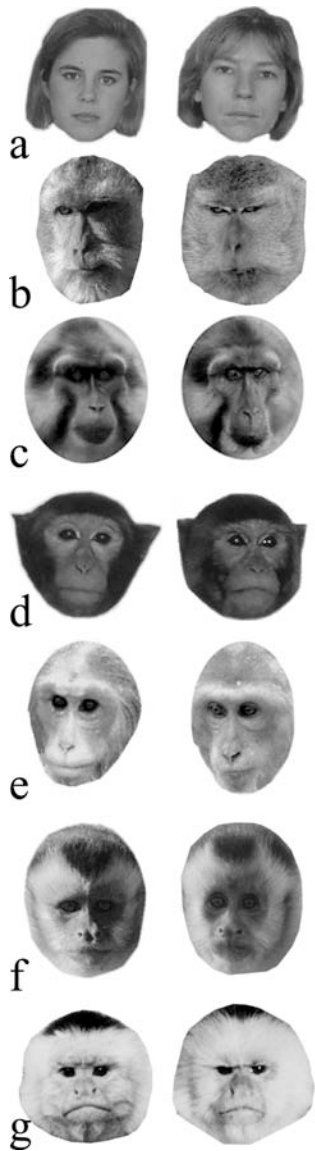
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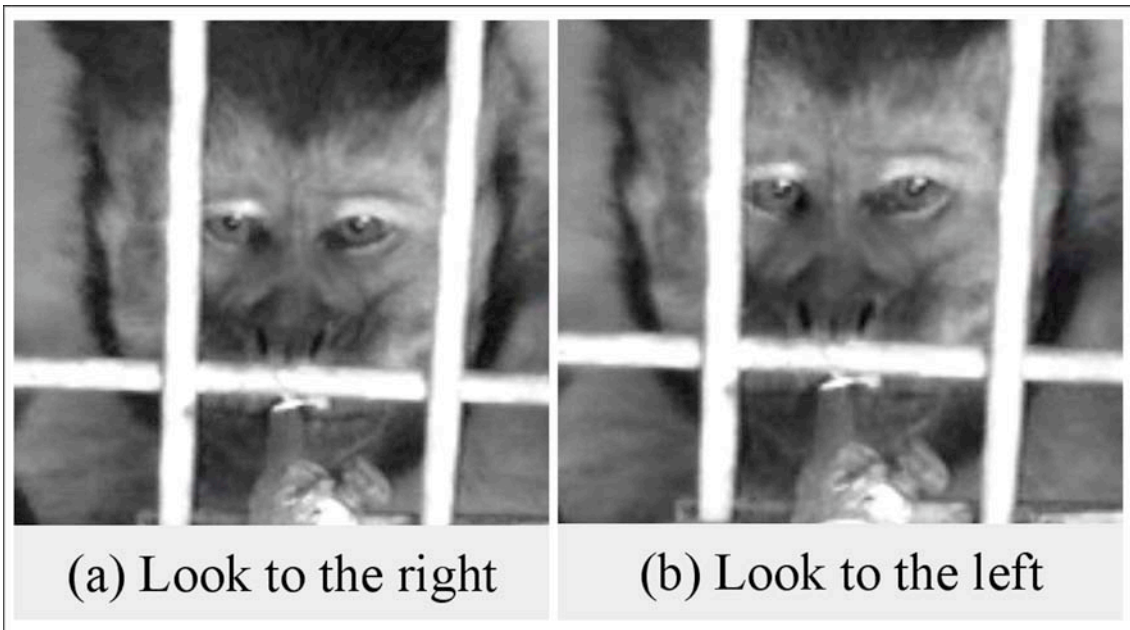
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