

1 **Title:**

2 *Conserved evolutionary history for quick detection of threatening faces*

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24

24

Abstract

25

26 Humans quickly recognize threats such as snakes and threatening faces, suggesting that human
27 ancestors evolved specialized visual systems to detect biologically relevant threat stimuli.
28 Although non-human primates also detect snakes quickly, it is unclear whether primates share
29 the efficient visual systems to process the threatening faces of their conspecifics. Primates may
30 not necessarily process conspecific threats by facial expressions, because threats from
31 conspecifics in natural situations are often accompanied by other cues such as threatening
32 actions (or attacks) and vocal calls. Here we show a similar threat superiority effect in both
33 humans and macaque Japanese monkeys. In visual search tasks, monkeys and humans both
34 respond to pictures of a threatening face of an unfamiliar adult male monkey among neutral
35 faces faster than to pictures of a neutral face among threatening faces. The monkeys' response
36 times to detect the deviant pictures of the no-face stimulus among threat faces were not slower
37 than those among the neutral faces. These results provide the first evidence that monkeys have
38 an attentional bias toward the threatening faces of conspecifics and suggest that threatening
39 faces are evolutionarily relevant fear stimuli. The sub-cortical visual systems in primates likely
40 processes not only snakes, but also more general biological threat relevant stimuli, including
41 threatening conspecific faces.

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Key words:

44 macaque monkey; threatening face; social threat; attentional bias; threat superiority effect

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46 Humans quickly recognize biologically threatening stimuli, such as snakes and threatening
47 faces (Hansen and Hansen 1988; Öhman et al. 2001; Masataka et al. 2010). A recent study
48 showed that snake-naïve monkeys responded more quickly to pictures of snakes among flowers
49 than vice versa in visual search tasks (Shibasaki and Kawai 2009). A neuroscience study
50 revealed that the pulvinar in the sub-cortical visual pathway plays a critical role in the
51 processing of images of snakes (LeDoux 1996). This neural system is assumed to help
52 mammals protect themselves against a variety of threats such as striking predators (i.e., snakes)
53 and angry conspecifics (Öhman and Mineka 2001). Isbell (2009) further hypothesized that the
54 visual system of ancestral primates has evolved to efficiently detect their major deadly
55 predatory threat, snakes. So far, empirical evidence has supported this snake detection
56 hypothesis by showing that pictures of snakes are detected faster in human adults (Hansen and
57 Hansen 1988) human children (Masataka et al. 2010; Hayakawa et al. 2011) and even
58 snake-naïve Japanese monkeys (Shibasaki and Kawai 2009) in similar visual search tasks.

59 These results lead researchers to posit that a preattentive and automatic bias toward
60 threatening stimuli exists because of its evolutionary relevance (Öhman et al. 2001; Öhman and
61 Mineka 2001). Öhman and colleagues extend this evolutionary framework to social threats by
62 relating them to the behavioural system controlling interactions between members of social
63 groups (Öhman et al. 2012). Although a large body of research has shown that threatening faces
64 are detected quickly (i.e., the threat-superiority effect), it is still unknown whether the
65 threat-superiority effect is present in non-human primates. Indeed, non-human primates may not
66 necessarily attend to the visual cues of an angry conspecific's face, because conspecific threats
67 in natural situations are always accompanied by other cues (e.g., aggressive actions and loud
68 calls). Therefore, non-human primates may not rely on their visual system to detect conspecific
69 threats. So far, there is no evidence for primates' quick detection of conspecifics' threatening
70 faces, despite many human studies showing this phenomenon.

71 Monkeys can extract a variety of information from photographs of conspecifics' faces. For
72 instance, Japanese monkeys can discriminate sex by the pictures of conspecifics' faces (Koba &
73 Izumi, 2006), rhesus monkeys are able to use facial cues to discriminate unfamiliar conspecifics
74 (Parr, Winslow, Hopkins, & de Waal, 2000), crested macaques identify individuals (Micheletta,
75 Whitehouse, Parr, Marshman, Engelhardt, & Waller, 2015), monkeys recognize the faces of
76 group mates in photographs (Pokorny & de Waal, 2009), infant rhesus monkeys look longer at a
77 threatening face than a neutral face of a conspecific (Mandalaywala, Parker, & Maestriperi,
78 2014), and rhesus monkeys can match facial expressions in pictures of conspecifics (Parr &
79 Heintz, 2009). A previous study, which compared static and dynamic video images of
80 conspecifics emotional faces, demonstrated that motion did not affect the monkeys' viewing
81 patterns to expressive facial displays (Nahm, Perret, Amaral, & Albright, 1997). Thus, we
82 assume that monkeys recognize photographs of faces as functional synonyms to real faces. It
83 should be mentioned that monkeys reared in isolation from birth displayed fear responses to
84 pictures of threatening conspecifics, suggesting that 'visual stimulation involved in threat
85 behavior appears to function as an "innate releasing stimulus" for fearful behavior' (Sakett,
86 1966, p. 1473).

87 The purpose of the present study was to examine whether Japanese monkeys and humans
88 recognize an unfamiliar monkey's threatening faces among neutral faces faster than the
89 converse.

90

91 **Methods**

92 Prior to the experiment, the face pictures were taken from an unfamiliar male Japanese
93 monkey, who was born and reared apart from the subjects in this study. Therefore, the subjects
94 had no prior experience with this model monkey. The model monkey was a fully grown adult
95 (12-year-old) male and was rated as the most dominant male in his animal room by two
96 independent animal caretakers. Half of pictures (320 x 240 pixel) were of a neutral face and the
97 other half showed a threatening face. The thirty-six pictures used in the experiment were chosen

98 because the type of facial expression was independently agreed upon by two reviewers, who
99 had more than eight years of experience with monkeys. The faces were extracted from the
100 background and converted to grayscale and matched for their luminance (Figure 1a, b).

101 The monkey experiment used three female Japanese monkeys (*Macaca fuscata*). They were
102 3 ('Pero' and 'Ume') and 5 ('Shiba') years old. They were housed individually in cages with ad
103 libitum water access. Daily food requirements (biscuits and vegetables) were delivered after
104 each experimental session and no restrictions on food were imposed. Our study complied with
105 current Japanese law and guidelines approved by the ethics committee of the Primate Research
106 Institute of Kyoto University.

107 The basic procedure was similar to a previous study of visual search tasks with pictures
108 of snakes (Shibasaki and Kawai 2009). The three monkeys performed a visual search task
109 with adult monkey faces. The monkeys were required to touch one deviant picture (e.g.,
110 one threatening face) on a 15-inch touch-sensitive monitor in the operant chamber (70 × 61
111 × 70 cm) from among 8 pictures of a different category (e.g., neutral faces) to receive a
112 reward.

113 *Face stimulus condition:* Pictures were presented as a nine-picture matrix in blocks of either
114 threat-relevant or threat-irrelevant targets. A block consisted of 72 trials comprising a
115 quasi-random sequence, altered each day. The learning criterion was set at a performance
116 rate of > 90% in three consecutive blocks for each target condition. After each monkey
117 reached the target accuracy, data were collected for 6 consecutive days (a total of 432 trial
118 per subject).

119 *No-face stimulus condition:* This condition was added to examine whether the monkeys
120 responded more slowly to the neutral face targets because of the aversive nature of the
121 screen showing an array of threatening faces. Almost two years after testing the face
122 stimulus condition (33 months for Shiba, 38 months for Pero, and 37 months for Ume), the
123 three monkeys were tested again with new target pictures of a no-face stimulus without
124 biological significance (i.e. pictures of computers that were luminance-matched to the face

125 pictures) among either threatening or neutral faces. The types of background faces were
126 alternated each day. The other procedures were same as in the face stimulus condition.

127 Human participants were 31 students (21 female, 10 male) with normal or
128 corrected-to-normal vision. All participants provided written informed consent. Although
129 human participants engaged in essentially the same visual search task with the same stimuli
130 as the monkey experiment of the face stimulus condition, there were slight differences in
131 procedure. As in most studies on threatening face effects, we required the participants to
132 judge whether the matrix contains one deviant item or all the same category item by
133 pressing keys. The matrices consisted of either nine-pictures or four-pictures presented on
134 the corners of the matrices. Half of the matrices were one-deviant matrices (as in the
135 monkey experiment), while the remaining matrices were same-category matrices where all
136 pictured faces expressed the same emotion. A session consisted of 136 trials comprising a
137 random sequence of 64 four-picture matrices and 72 nine-picture matrices. Participants
138 were required to press keys corresponding to their judgment as to whether the matrix
139 contained one deviant facial expression or all the same expression. If the participant made
140 an error, feedback consisting of a beep sound for 1 sec was provided. No feedback was
141 provided for the correct response.

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144 Results

145 *Face stimulus condition:* The number of sessions to reach the learning criterion was 110
146 sessions for Shiba, 81 sessions for Pero, and 57 sessions for Ume. Incorrect responses were
147 classified as errors and excluded from the following analysis. The monkeys' error rates
148 were 7.6% (Shiba) and 5.0% (Pero and Ume). As shown in Figure 1, the median latencies
149 for the three monkeys to detect the deviant pictures of a threatening face were faster than to
150 detect the deviant pictures of a neutral face (Mann-Whitney's U-tests: Shiba, $U = 19931.5$, Z
151 $= 2.62$, $p < .01$; Pero, $U = 18471.5$, $Z = 3.67$, $p < .001$; Ume, $U = 18369.5$, $Z = 3.82$, p

152 < .001). As a whole, the three monkeys detected threatening faces from neutral faces faster
153 than vice versa ($Z = 5.58, p < .001$).

154 *No-face stimulus condition*: Although the monkeys had not watched the pictures of the
155 monkey faces for almost two years, they reached the learning criterion within a few
156 sessions. The monkeys found the target pictures of the non-face stimulus (computer
157 pictures) among the threatening faces as quickly as they did among the neutral faces. The
158 median latencies to detect the no-face target pictures among the threat and neutral faces
159 were 912 ms and 890 ms for Shiba, 749 ms and 757 ms for Pero, and 687 ms and 673 ms
160 for Ume, respectively. These latencies did not differ significantly between the two types of
161 background face stimuli (Mann-Whitney's U -tests: Shiba, $U = 22275.0, Z = 0.81, p = .41$;
162 Pero, $U = 21839.5, Z = 1.14, p = .25$; Ume, $U = 23328.0, Z = 0.11, p = .91$).

163 Human participants also made few errors (2.8% overall). The right part of Figure 1c
164 shows the median average latencies for each participant to identify the deviant faces in
165 matrices. Participants responded faster when detecting the deviant picture of a threatening
166 face than a neutral face (Wilcoxon exact signed-rank tests: $Z = -4.30, p < .001$).

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Discussion

169 The present study clearly demonstrates that the monkeys detect a deviant picture of a
170 threatening face among neutral faces faster than vice versa. Although previous studies
171 showed that monkeys can learn to categorize expressions of conspecifics (Kanazawa 1996),
172 this study provides the first evidence for the threat superiority effect in non-human primates.
173 The monkeys' response times to detect the deviant pictures of the no-face stimulus among
174 the threat faces were not slower than those among the neutral faces. Therefore the slower
175 responses to the neutral face target among the threat faces (i.e. quicker detection of threat
176 faces) cannot be attributed to a more cautious approach to the aversive screen when it was
177 showing an array of threatening faces. The present study suggests facial expression alone
178 may be sufficient to alert monkeys to threats from conspecifics. A cross-species

179 comparison of facial morphology and movement in humans and chimpanzees suggested the
180 homologies between two species (Vick et al. 2007). Given the close phylogenetic distance
181 between humans and Old World monkeys, humans and monkeys likely share homologous
182 mechanisms to detect threats efficiently.

183 Human participants also showed faster recognition of the threatening faces of a
184 monkey. Although the human face has a more complex musculature than other primates
185 that allows more complex facial expressions, the basic human facial displays are probably
186 similar to those of other primates. Thus human participants would respond to threatening
187 faces of monkeys based on their basic features similar to human threatening face (e.g.,
188 open-mouth).

189 As monkeys in this study had a little prior experiences of interacting with conspecifics,
190 it is not clear to what extent learning contributes to the quick detection of the threatening
191 faces. It should be mentioned that, however, a previous study showed that macaque
192 monkeys reared in isolation from birth displayed fear responses to the pictures of
193 threatening conspecifics, suggesting that ‘visual stimulation involved in threat behavior
194 appears to function as an “innate releasing stimulus” for fearful behavior’ (Sakett, 1966,
195 Science, p. 1473), and therefore interaction with others seems not to be necessary for
196 threatening face recognition. In other words, the monkeys seem to be predisposed to
197 respond threatening faces innately.

198 One could interpret the present results in terms of possible habituation effects. As the
199 monkeys can see other monkeys in the same breeding room, seeing neutral faces is in some
200 way more common in the monkeys’ experience than seeing threatening faces. The
201 monkeys’ reduced attention to familiar faces might lead to a quicker detection of
202 threatening (non-habituated) faces. However, monkeys do not seem to attend to faces
203 merely because of their rarity. For instance, rhesus monkeys looked longer at real or
204 unrealistic synthetic faces than at realistic faces of conspecifics (Steckenfinger &
205 Ghazanfar, 2009). If monkeys displayed reduced attention to familiar faces, they would

206 spend the shortest time to look at real faces; however, this was not the case. In the visual
207 search task of a previous study, a chimpanzee performed more quickly when the target was
208 a direct-gaze face surrounded by averted-gaze faces of humans than when it was an
209 averted-gaze face of the same individuals (Tomonaga & Imura, 2010). The chimpanzee
210 should have less experience in looking at averted-gaze faces. Humans also detected
211 schematic threatening, angry faces more quickly than other negative (sad or ‘scheming’) or
212 neutral faces (Öhman, Lundqvist, & Esteves, 2001). These studies suggest that a potential
213 habituation effect to neutral faces could not have yielded the quick detection of threatening
214 faces of this study.

215 It should be noted that not only primates but a wide variety of vertebrate species also
216 show a general tendency to preferentially attend to faces or even to other non-biological
217 face-like stimuli (Salva & Vallortigara, 2015). The preference for faces or face-like stimuli
218 is observed in newborns of many species (Johnson, 1992) and in newly hatched face-naïve
219 chicks (Salva, Farroni, Regolin, Vallortigara, & Johnson, 2011), suggesting that newborn
220 vertebrates have a visual predisposition to attend to the head region of animated creatures
221 (i.e. the face). The ability to engage in a social exchange with adult caregivers is crucial for
222 a human newborn to identify communicative partners and establish eye contact with them.

223 In contrast, some avian species are spontaneously frightened by the presence of stimuli
224 resembling a pair of eyes (e.g. Scaife, 1976). Factors such as presence of two eyes aligned
225 on the same horizontal line and presence of both iris and pupil are crucial to elicit a fear
226 response in chicks (Jones, 1980). Conspicuous eyes are a distinctive trait of many potential
227 predators, in which the dark spot (pupil or iris) contrasts the lighter circle (iris/sclera or
228 lighter pigmentation). For precocial species such as chicks, the capacity not only to
229 recognize social partners but also to detect potential predators that are attentive to the chick
230 is crucial for survival (Salva, Regolin, & Vallortigara, 2012). However, the same innate
231 fear for such stimuli that mark potential predators would be useless in newborns of humans
232 and other altricial species. As most primates are altricial species, they have evolved to

233 detect threats such as recognizing facial expressions. Human infants as young as 4-months
234 old can discriminate between direct and averted gaze when the adult face displays an angry
235 expression but not when it shows a neutral or happy expression (Striano, Kopp, Grossmann,
236 & Reid, 2006). Obviously, human infants can process angry expressions relating to the self.
237 Attention to threatening faces may be a further elaboration of the response to face-like
238 stimuli in primates.

239 One might be able to explain the present search asymmetry effect without referring to
240 social threat, as the search asymmetry effect can be produced by various factors. In this
241 study, simple features such as distributions of high contrast regions in the pictures might
242 result in the search asymmetry. For instance, the faces with an open mouth contain a salient
243 visual cue that is absent in the faces with a closed mouth. The explanations based on
244 low-level features for threat superiority were excluded in human studies. Fox and
245 Damjanovic (2006) demonstrated the threat superiority effect with photographs of human
246 faces, which was not observed when the faces were inverted, suggesting that some
247 low-level visual features do not play a major role in producing the threat superiority effect
248 in humans. Face inversion may simply slow down the processing of emotion so that there is
249 not enough time for a threat superiority effect to arise. However, Tipples, Atkinson, and
250 Young (2002) found that threatening faces with V-shaped eyebrows (angry and scheming
251 expressions) were detected more quickly than non-threatening faces with Λ -shaped
252 eyebrows (happy and sad expressions), and that no advantage was found for V-shaped
253 eyebrows presented in a non-face like stimulus. Therefore, the threat superiority effect does
254 not seem to be due to perceptual features unrelated to the face (see also Fox, Lester, Russo,
255 Bowles, Pichler, & Dutton, 2000; Öhman et al., 2001). Although this study presented
256 neither inverted nor schematic faces with the same visual properties, simple visual features
257 are less likely to produce the reported threat superiority effect, as shown in previous studies
258 by human participants.

259 Snakes have been regarded by some to be the prototypical evolutionarily fear-relevant
260 stimuli (Isbell 2009), with the relevance of threatening faces still unclear. Öhman and
261 colleagues postulated that fear of threatening faces has its origin in a social submissiveness
262 system, the function of which is to detect and avoid potentially serious physical damage in
263 an active dominance struggle with conspecifics (Öhman et al. 2012). To further understand
264 the role of a social submissiveness system in attention bias to threatening faces, it seems
265 fruitful to assess whether primates that live only with family instead of a mixed-family
266 conspecific group, thus having no hierarchy (i.e., marmosets or gibbons), show a threat
267 superiority effect for threatening faces.

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Figure Caption

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351 **Figure 1.** In the two upper panels both the target and the distracter faces were taken from the
352 same monkey. (a) The neutral face target is presented among emotional (angry) distracter faces.
353 (b) The emotional face target is presented among neutral distracter faces. (c) Median reaction
354 times are depicted as bold horizontal bars inside the boxes. The lower and upper lines of each
355 box represent the first and third quantiles, respectively. The asterisks indicate
356 significant differences at the 0.01 (**) and the 0.001 (***) probability level.

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