

Title	Thatcher Effect in Monkeys Demonstrates Conservation of Face Perception across Primates
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1 **Thatcher effect in monkeys**
2 **demonstrates conservation of**
3 **face perception across primates**
4

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17 Running head: Monkey Thatcher

18

19 **Summary**

20 Accurate recognition of individuals is a foundation of social cognition. The remarkable ability of
21 humans to distinguish among thousands of similar faces depends on sensitivity to unique
22 configurations of facial features, including subtle differences in the relative placement of the
23 eyes and mouth [1, 2]. Determining whether similar perceptual processes underlie individual
24 recognition in nonhuman primates is important for both the study of cognitive evolution and the
25 appropriate use of primate models in social cognition research. In humans, some of the best
26 evidence for a keen sensitivity to the configuration of features in faces comes from the “Thatcher
27 Effect”. This effect shows that it is difficult to detect changes in the orientation of the eyes and
28 mouth in an image of an inverted face, even though identical changes are unmistakable in an
29 upright face [3, 4]. Here, we demonstrate for the first time that a nonhuman primate species also
30 shows the Thatcher Effect. This direct evidence of configural face perception in monkeys,
31 collected under testing conditions that closely parallel those used with humans, indicates that
32 perceptual mechanisms for individual recognition have been conserved through primate
33 cognitive evolution.

34

35

36 **Results and Discussion**

37 Look briefly at Figure 1, which contains two pictures of the same person. Now turn the page
38 upside down and look again. While one face may look unusual in both orientations, the
39 difference between the faces is especially striking when they are viewed upright (i.e. when the
40 page is upside down). This phenomenon is called the Thatcher Effect because it was first
41 demonstrated using an image of the face of Margaret Thatcher [3]. Note that the two images
42 share the same facial features placed in the same regions of the face. The images differ in the
43 relations among these features; the orientation of the eyes and mouth is altered in the
44 “thatcherized” face. The fact that we can more easily detect manipulation of the configuration of
45 features in upright faces demonstrates two properties of human face perception: 1) we normally
46 perceive faces configurally, which promotes sensitivity to the relative placement of facial
47 features, and 2) configural perception is disrupted when a face is viewed upside down [3-7].
48 Because faces share many similar features they are difficult to differentiate based on features
49 alone. Distinguishing among a large number of faces is enhanced by sensitivity to unique
50 configurations of facial features, including subtle differences in the relative placement of the
51 eyes and mouth [1, 2]. Thus, the Thatcher Effect demonstrates a critical perceptual process
52 supporting individual recognition.

53 Consistent with the impaired perception of inverted faces demonstrated by the Thatcher Effect,

54 many studies of human perception have shown that faces are more easily recognized when
55 upright than when inverted [1, 8, 9]. Investigators of nonhuman primate perception have also
56 compared recognition and discrimination of upright and inverted faces, but with inconsistent
57 results. Some studies show superior perception of upright faces like that found in humans
58 (cotton-top tamarins [10]; pigtail macaques [11]; chimpanzees [12-15]; Japanese macaques [16];
59 rhesus macaques [17, 18]). However, in other studies no difference in accuracy with inverted and
60 upright faces was found (cotton-top tamarins [19]; longtail macaques [20, 21]; rhesus monkeys
61 [22, 23]; baboons [24]). The cause of the inconsistency is not clear, but there are at least two
62 reasons to be cautious in using these studies to evaluate the role of configural perception in
63 primate face recognition. First, configural face perception was not directly assessed in these
64 studies because the relations among facial features were not manipulated (but see [18], where
65 low and high pass filtering was used in an effort to isolate configural processing). Second, most
66 of these studies involved extensive training with a small set of images. Such training may
67 encourage subjects to discriminate faces by memorizing individual salient features (e.g., a dark
68 spot on the chin on one face that is absent from others) rather than by perceiving the
69 configuration of facial features, as monkeys might do in nature where they are confronted with
70 the many faces in their social group. Because findings have been inconsistent, and the
71 methodologies used to date may artificially encourage nonconfigural processing, the extent to

72 which configural perception underlies natural nonhuman primate face recognition is difficult to
73 determine from the existing literature.

74 We used the Thatcher Effect to directly assess configural face perception in rhesus monkeys
75 without explicit training. Because thatcherization involves manipulation of the configural
76 properties of faces, and the Thatcher Effect is revealed by comparing perception of upright and
77 inverted faces, this approach allows us to clearly evaluate the effect of face orientation on
78 configural face perception, should it occur in monkeys. Monkeys saw thatcherized and normal
79 monkey faces in a habituation-dishabituation paradigm. During the habituation phase of each test,
80 we presented one of six unaltered images of monkey faces either upright (Upright condition) or
81 inverted (Inverted condition) 10 times consecutively. The dishabituation phase followed, in
82 which the original (intact) and the thatcherized versions of the habituated face were presented in
83 the same orientation used in the habituation phase (Figure 2). The order of presentation of the
84 normal and the thatcherized images in the dishabituation phase was counterbalanced across the
85 subjects, and across tests with the two orientations of the six different stimulus monkey images.
86 Thus, twelve tests (six unfamiliar monkey faces, each presented in both the Upright and Inverted
87 orientation) were administered to each subject monkey. During both the habituation and the
88 dishabituation phases, a “beep” from a speaker located behind the monitor indicated to the
89 subject when an image was displayed. Each image was presented for 30 seconds with a 10 s

90 interval between images, during which the screen was black. Subjects' looking behavior was
91 video recorded and quantified by a coder blind to test condition later.

92 We expected a decrease in the time monkeys spent looking at a face over the course of the
93 habituation phase of each trial. Based on the results of studies of the Thatcher Effect in humans,
94 we hypothesized that if monkeys perceive faces configurally they should be surprised by the
95 unusual manipulation of the eyes and mouth in the thatcherized faces. Such surprise would
96 manifest in monkeys looking longer at thatcherized than intact faces during the dishabituation
97 phase of trials. Furthermore, if monkey face perception follows the pattern found in humans,
98 such dishabituation should be much more pronounced for upright than for inverted faces.

99 As expected, the monkeys showed decreased interest in both the upright and inverted images
100 of faces across the habituation trials, indicated by reduction in time spent looking at the images
101 (Figure 3, line graphs on the left side). From this habituated state, monkeys showed significantly
102 more dishabituation to the upright thatcherized faces than to the inverted thatcherized faces
103 (Figure 3, bar graphs on the right side). The difference in dishabituation demonstrates that the
104 manipulation of the orientation of the eyes and mouth was more salient in the upright faces,
105 constituting a Thatcher Effect in monkeys that parallels that seen in humans.

106 Because we used identical images in the upright and inverted conditions, the differences in
107 dishabituation cannot be explained by any idiosyncratic characteristics of our stimulus materials.

108 The orientation of the faces was the only difference between the two conditions. Our subjects
109 showed similar initial interest in upright and inverted faces and habituated equivalently to the
110 two types of stimuli (compare blue and red lines in Figure 3). The lack of significant
111 dishabituation in the inverted condition cannot, therefore, be explained by unsuccessful
112 habituation during the habituation phase. Instead, these results provide direct behavioral
113 evidence that, 1) monkeys perceive faces configurally and, 2) this configural processing is
114 disrupted when the face is inverted. Humans are likely to describe an upright thatcherized human
115 face as “gruesome.” While we cannot be certain whether or not the monkeys had similar
116 phenomenological experience while viewing the upright thatcherized monkey faces, the
117 behavioral results presented clearly demonstrate that the changes brought about by
118 thatcherization were more readily detected by the monkeys in upright faces. Future studies using
119 heart rate, pupil size, or other physiological measures might begin to address whether monkeys,
120 like humans, perceive thatcherized faces as alarming or gruesome.

121 We know of only two other studies of nonhuman species that have used thatcherized faces. In
122 apparent conflict with the present results, thatcherization of stimulus faces did not affect
123 accuracy in tests of perceptual competence in either study (pigeons, *Columba livia* [25]; baboons,
124 *Papio papio* [26]). However, both of these studies used a matching-to-sample paradigm that
125 required extensive pre-training. Extensive pre-training, particularly with a small set of images,

126 may cause subjects to use a few salient cues, rather than the configuration of facial features, to
127 identify stimulus faces. In contrast to the techniques used in the pigeon and baboon studies cited
128 above, in humans the Thatcher Effect is normally demonstrated as a spontaneous reaction,
129 outside the context of any explicit recognition or matching test [3, 4]. Such spontaneous
130 reactions likely better reflect normal face perception than do trained discriminations. According
131 to this analysis, failure to find the Thatcher Effect in earlier studies does not represent a
132 discontinuity between humans and nonhumans in the mechanisms of normal face perception, but
133 rather indicates changes in perception or attention brought about by extensive training with
134 specific stimuli. The present study is a direct test of configural face perception, and better
135 matches the spontaneous conditions under which the Thatcher Effect is observed in humans. It
136 also directly shows that configural perception is disrupted by face inversion in monkeys. Because
137 we did not train discrimination of the images we used, the behavior of our monkeys likely
138 reflects the same perceptual processes used in natural face perception.

139 This first demonstration of the Thatcher Effect in nonhuman animals is important because it
140 indicates conservation of configural face perception across primate species and suggests that this
141 mechanism for distinguishing among many similar faces may have evolved in an ancestor
142 common to humans and rhesus monkeys 30 million or more years ago [27]. It is likely that
143 previous findings that appear inconsistent with configural processing, such as the lack of an

144 “inversion effect”, are training artifacts and do not reflect true species differences in face
145 perception among primates. However, it will be of interest to determine the extent to which the
146 Thatcher Effect reflects species-specific specializations of face perception. This question can
147 best be addressed by “crossed” comparative studies in which two different species are tested with
148 thatcherized faces of both their own and the other species. Our behavioral evidence reinforces
149 recent comparative neuroimaging results showing similar specialized neural substrates for face
150 perception between monkeys and humans [28] (but see also [29], for a different view). It will be
151 necessary to repeat behavioral tests on other species to determine how widespread configural
152 face perception is phylogenetically, and whether it has evolved only in species for which
153 individual recognition is critical.

154 **Experimental Procedures**

155 We studied four 4-year-old male rhesus macaque monkeys (*Macaca mulatta*) raised for 2 to 3
156 years in large social groups at the Yerkes National Primate Research Center. In the lab they were
157 pair-housed, permitted full social contact with their cagemates outside of testing periods, and had
158 visual and auditory contact with additional monkeys living in the same room. All procedures
159 used were approved by the Institutional Animal Care and Use Committee at Emory University.

160 Monkeys were tested in a cage (60cmW*72.5cmL*81.3cmH), placed 80 cm away from a 19
161 inch LCD color monitor inside a sound attenuating booth. A camera was attached to the monitor

162 to record the looking behavior of subjects. Stimuli were color frontal views of six unfamiliar
163 male rhesus monkey faces and the thatcherized versions of these faces shown on a black
164 background (450 pixel * 550 pixels, Figure 4). Testing was controlled by custom software
165 written using Presentation© (Neurobehavioral Systems, Albany, CA).

166 Videos of subjects were analyzed after all testing was complete. The first author separated the
167 14 image presentations from each test (10 presentations in the habituation phase and 4 from the
168 dishabituation phase) into separate digital video files, resulting in 168 files for each subject (14
169 presentations per test * 6 stimulus monkeys * two orientations). Each clip was arbitrarily named
170 and the order of the clips was randomized. Because videos were taken from the position of the
171 display monitor, they did not reveal which image was presented to the subject monkey,
172 permitting blind coding by the second author. The video files were examined frame by frame and
173 the monkey was coded as looking at the monitor when a pupil was directed at the camera,
174 irrespective of head and body orientation. One 10 s presentation of an intact inverted face was
175 not captured on video due to a technical problem and was not included in the calculation of
176 average looking times.

177

178

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253

254 **Figure legends**

255 **Fig. 1. Example of the Thatcher Effect.**

256 The face on the left is unaltered while the face on the right has been “thatcherized” by inverting
257 the mouth and eyes relative to the rest of the face. Contrast your perception of the faces viewed
258 inverted, as shown, and after rotating the page to make the faces upright. Thatcherization is most
259 obvious when faces are viewed upright.

260

261 **Fig. 2. Schematic of the habituation-dishabituation paradigm.**

262 Half of tests used upright images (left side) and the other half inverted images (right side). Each
263 image was presented for 30 seconds, separated from the next presentation by 10 seconds with no
264 image. Each presentation was cued by a “beep.” Ten presentations of a given image constituted
265 the habituation phase (top). The habituated (intact) and thatcherized faces were presented twice
266 each in the dishabituation phase in an ABBA sequence (bottom). Whether an intact or
267 thatcherized face was shown first in the dishabituation phase was counter-balanced across tests
268 and monkeys.

269

270

271 **Fig. 3. Monkeys look longer at upright than at inverted thatcherized faces.**

272 Mean time spent looking at the monitor in the habituation phase (left side, line graphs) and the
273 dishabituation phase (right side, bar graphs). The upright condition is shown in solid blue; the
274 inverted condition is shown in dashed or hatched red. Error bars are standard error. Looking
275 times were calculated in milliseconds (based on frame by frame analysis of digital video) and
276 then log transformed to approximate normality. Monkeys habituated indistinguishably to upright
277 and inverted faces during the habituation phase (Repeated measures ANOVA: Trial Block, $F_{1,3} =$
278 $51.384, p = 0.006$; Orientation, $F_{1,3} = 0.976, p = 0.396$; Trial Block X Orientation, $F_{1,3} = 4.483, p$
279 $= 0.125$). The Thatcher Effect is evident in the dishabituation phase by the significant interaction
280 between face type (thatcherized or intact) and orientation (Repeated measures ANOVA: Face
281 Type X Orientation, $F_{1,3} = 64.714, p = 0.004$; Face Type, $F_{1,3} = 12.964, p = 0.037$; Orientation,
282 $F_{1,3} = 7.946, p = 0.067$). To confirm that the significant Face Type X Orientation interaction was
283 caused by longer looking times for upright thatcherized faces, we conducted two posthoc tests.
284 Monkeys looked significantly longer at upright than inverted thatcherized faces but looked
285 equally long at upright and inverted intact faces (two-tailed paired t-tests, thatcherized faces: $t_3 =$
286 $7.167, p = 0.006$; intact faces: $t_3 = 1.227, p = 0.307$).

287

288

289 **Fig. 4. Intact and thatcherized monkey faces used.**

290 The left hand column shows all six intact monkey faces used; the right column shows the
291 thatcherized version of each of these faces.

292

Figure1

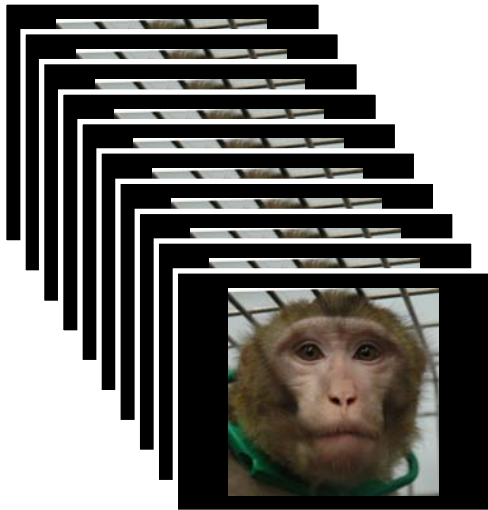


Figure2

Upright Condition

Inverted Condition

Habituation
Phase



Dishabituation
Phase



Figure3

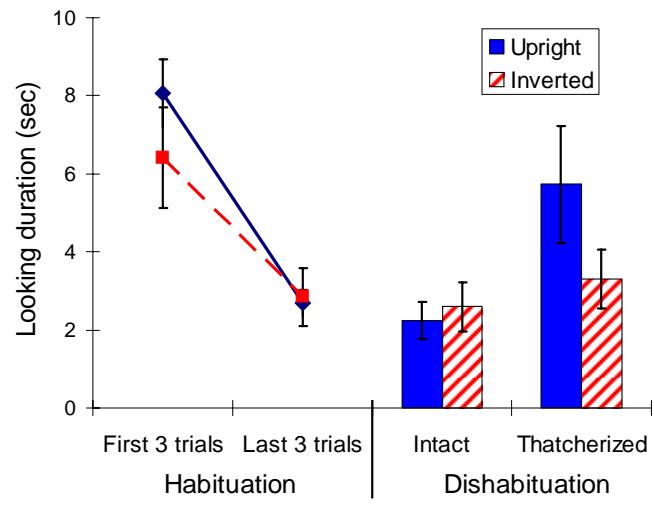


Figure4

